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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE.
VOL. XXII. No. 1.

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OBSERVATIONS ON BUDDING IN PALUDICELLA AND SOME OTHER BRYOZOA.

BY C. B. DAVENPORT.

WITH TWELVE PLATES.

CAMBRIDGE, U.S.A.:
PRINTED FOR THE MUSEUM.
DECEMBER 1891.

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No. 1. — *Observations on Budding in Paludicella and some other Bryozoa.* By C. B. Davenport.[1]

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A. SPECIAL PART.

I. Introduction.

The somewhat heterogeneous studies here brought together have been prosecuted at different times and in different places, as opportunity for getting light on the problem of non-sexual reproduction as exhibited in the group of Bryozoa has presented itself.

While studies on the fresh water species were pursued chiefly here at Cambridge, those on marine Bryozoa were made while occupying one of the tables of the Museum at the United States Fish Commission Laboratory at Wood's Holl, Mass., during the summer of 1889, and while at Mr Agassiz's Newport Laboratory during the summer of 1890. To my instructor, Dr. E. L. Mark, for many valuable suggestions during the progress of my work and the writing of this paper, to Mr. Alexander Agassiz, for the kind hospitality accorded me at his Newport Laboratory, and to Hon. Marshall McDonald, United States Commissioner of Fish and Fisheries, and Dr. H. V. Wilson, Assistant at Wood's Holl, for favors shown me while at the Wood's Holl Laboratory, I make grateful acknowledgment of my indebtedness.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXVIII.

A word as to localities. The marine Bryozoa were found especially abundant at Newport on floating eel-grass in the cove and on the piles of the wharf. The embryos of Cristatella and Plumatella were found in colonies which literally covered the bottom of some parts of the south or shady side of Trinity Lake, Pound Ridge, New York. They occur especially in densely shaded and fairly deep water near the shore.

The Gymnolæmata present many difficulties to finer technique. They possess a chitinous covering, often very thick, and frequently, in addition, a calcarous skeleton. When the latter is present, picro-nitric acid mixed with sea water is a fairly good fixing reagent; when it is absent, hot corrosive sublimate was most serviceable. The objects must be transferred through the grades of alcohol with extreme caution, to prevent the collapse of the ectocyst. I used the chloroform-paraffin method of embedding in order to make transfers more gradual at this stage. Some difficulty was experienced in staining such small objects on the slide, since the tissues are very loosely associated; and on the other hand *in toto* staining is unsatisfactory in some cases, owing to impenetrability of the ectocyst. Often it was necessary to open the body cavity of each individual by means of a sharp knife or needle. The best results were obtained with alcoholic dyes like Kleinenberg's hæmatoxylin and Mayer's cochineal; although Ehrlich's hæmatoxylin was often used with success.

II. Budding in Paludicella.

1. ARCHITECTURE OF THE STOCK.

Paludicella, as is well known, occurs in quiet streams and forms stocks on the under surfaces of stones and other objects. Seen with the naked eye these stocks appear as a fine lacework, composed of constantly branching lines of individuals. Some of the stocks which I have measured are over 25 mm. in length along their greatest diameter.

When the stock is studied more carefully, it is seen that the individuals which compose it are arranged one in front of the other, forming lines. (Figs. 1, 2, 2ª.) We may distinguish (1) a single primary branch, which forms a continuous line from the oldest individual, which has been derived directly from the egg, to the terminal one; and (2) secondary branches, which arise from the individuals of the primary branch and at right angles to their axes. Typically, a secondary branch arises from both the right and left sides of each adult member of the primary branch. but in some cases the secondary branch of only one side appears to be formed. The secondary branches are composed, like the primary, of a continuous line of individuals placed end to end. These in turn give rise to tertiary branches, which run out at right angles to the right and to the left of the secondary ones, and hence parallel to the primary branches. Quaternary branches may occur in like manner, but I have never seen branches of a higher order than the fourth. All of these branches may lie in one plane, but frequently some of the lateral buds are so placed that they give origin to secondary branches which rise above the plane of the object upon which the stock lies. A study of Figure 1 and the corresponding diagram, Figure 2, reveals some additional facts. The two lateral buds of an individual do not arise at the same time, and there is a tendency for the first, and therefore oldest and most developed, secondary branches to arise alternately on opposite sides of the primary branch. This last rule has many exceptions, however.

The long axis of the individual coincides with that of its branch; the sagittal plane lies in that axis, and at right angles to the substratum. The atrial opening is near the distal end of the individual in the sagittal plane, and is turned away from the substratum. The anal aspect of the polypide is placed nearer the tip of the branch, — hence distad; the mouth, on the contrary, proximad.

A very casual observation shows that not all branches nor all individuals are of the same size. The shortest and therefore youngest branches are placed most distally, and are seen as small buds. The terminal individuals of the branches are also evidently less well developed than the more proximal ones. The adult individuals measure from 1.5 to 2.0 mm. in length and from 0.30 to 0.35 mm. in width. The younger individuals differ from the older in form also. The outline of the adult branch, looked at from the side, and disregarding the atrial opening, is formed by a series of beautiful sigmoid curves (Fig. 9). The concave and convex points of the upper and lower sides of an individual are not placed exactly opposite each other, and the lower (abatrial) side approximates more nearly to a straight line. The point at which the upper and lower curves most nearly approach each other is where the separation of two individuals takes place; that at which they are farthest apart is the middle of the zoœcium, occupied by the polypide and sexual organs. The outlines of the young zoœcia are straighter, and their breadth is considerably less than that of the adult.

From what we have already seen, the method of growth of the stock is perfectly evident: it is by the formation of new median buds at the tips of existing branches, and of new branches from lateral buds. In order to understand the origin of the individuals of the primary branches, to which subject we will first turn our attention, we must study the tips of the branches.

2. Histology of the Budding Region.

Figures 7–9 will serve to show more in detail the method of formation of new terminal individuals. We find in these cases one polypide already pretty well developed and attached to the body wall by means of the kamptoderm at about the point at which the pyramidal muscles (*mu. pyr.*) are seen to be forming. That portion of the animal which extends from about the region of formation of the muscles to a point a little proximad of the tip represents the region which will go to form the new individual. The tip itself, for reasons which will presently appear, is not to be included in the terminal individual. The tip of the branch is to be regarded as homologous with the margin of the corm in corm-building genera of Gymnolæmata. Figures 7–9 (*gn.*) also show the position of the bud which is to produce the polypide. By consulting first Figure 9, in which the polypide bud is apparent, the significance of the swellings of the body wall in Figures 8 and 7 becomes clear.

Figure 14 (Plate II.) represents a stage in the development of the polypide bud, somewhat later than that shown in Figure 9, and this may serve us as a starting point in our study of the origin of a new individual, and, first of all, of the new polypide. The whole of Figure 14, from the tip down to the neck of the older polypide (*cev. pyd.*), may be divided, for convenience, into three zones: first, that distad of the young bud, which may be called the *tip of the branch* (Fig. 14, α to β); secondly, the region of the bud itself, which may be called the *gemmiparous zone* (β to γ); and thirdly, the region between this last zone and the neck of the older polypide, which, for want of a better name, may be called the *proximal zone* (γ to δ). In the formation of a new polypide between α and β, that region will in turn become divisible into the three zones just named, exactly as the region *a* to *δ* represented the *tip* of the branch when the older polypide, whose neck is shown at *cev. pyd.*, was of the age that the younger bud is now. It will be necessary first of all to study carefully each of these three regions before treating of their origin and fate.

The *tip of the branch* consists of the two layers of cells which are found in other parts of the body wall, — the ectoderm and the mesoderm, as the cœlomic epithelium may, for brevity's sake, be called. The cells of the ectoderm at the extreme tip (Plate I. Fig. 6) are greatly elongated, forming a columnar epithelium. There are about 25 or 30 of the larger cells. They have a length of 28 μ to 32 μ, and a diameter of about 4 μ. They possess an ovoid nucleus averaging 5.7 μ by 2.6 μ, which lies in the middle of the cell but slightly nearer the cœlomic epithelium than the cuticula. It possesses a large nucleolus over 1 μ in diameter, which often appears stellate owing to the threads of plasma surrounding and proceeding from it and forming a nuclear network. As the figure shows, the plasma of the cell is filled with large, apparently deeply stained granules, some of the largest being over 0.6 μ in diameter. The coarser granules lie chiefly in the immediate vicinity of the nucleus, but are also found arranged in long lines at right angles to the surface throughout the greater part of the cell, becoming finer the farther they lie from the nucleus. A fine network can sometimes be made out between the large granules, but this appearance is more evident at the peripheral portion of the cell, where there are no large granules. At the outer and inner ends of the cells one finds large vacuoles, the largest of which are of about the same size as the nucleus; these become smaller the nearer they lie to the nucleus. In many cases the larger vacuoles are each seen to be partly filled by a body which stains slightly, and, as focusing determines, is more highly refractive than the plasma. Similar highly refracting, slightly staining granules are found in, and in fact often composing, the smaller "vacuoles." Owing to the fact that the deeply staining granules lie near the nuclei, and that the vacuolated and finely granular plasma lies more remote, there is a very marked deeply staining band occupying the middle of the ectodermal layer, and having about four tenths the thickness of the whole layer.

At the outer ends of the cells, and doubtless secreted by them, there is a cuticula about 1 μ thick. Its inner surface is sharply marked off from the underlying plasma; its outer surface is less sharp, and there are usually very minute particles of dirt attached to it (not represented in the figure). The whole cuticula forms in section a continuous band of substance, which stains deeply in Ehrlich's hæmatoxylin (but not at all in alum cochineal), and covers nearly the whole tip. Looked at from the surface after staining in hæmatoxylin, it appears uniformly dark. The mesoderm of the tip is highly modified, and a description of it will be more instructive after I shall have described the normal cœlomic epithelium, as I shall do later.

Passing from the extreme tip towards β (Fig. 14), one finds the ectodermal cells gradually changing in form, size, and structure, and becoming slightly broader, and very much shorter. Their nuclei lie near the inner ends of the cells, possess a thick "nuclear membrane," and are more nearly spherical than those of the columnar cells, but of about the same size. They each possess one very large, centrally placed nucleolus, whose diameter equals and sometimes exceeds one third that of the nucleus, and whose outline is often somewhat stellate. Outside of the nucleus in the cell body there are fewer and fewer vacuoles as we pass from the tip, but the plasma is still coarsely granular, and here, as before, these stained granules surround the nucleus. It is now the regions between cells rather than those at the inner and outer ends which remain unstained, so that the cells are separated from one another by light spaces.

The mesodermal layer becomes somewhat thinner than at the tip, that is to say, its cells are flattened. The nuclei are elongated in the axis of the branch, and average about 4 μ by 2.2 μ. They possess one spherical nucleolus, whose diameter is about two thirds of the minor axis of the nucleus. Small, clear vacuoles often with highly refractive spherical bodies are abundant in the cell protoplasm, which stains as a whole less deeply than does the ectoderm. Such highly vacuolated elements will be called *reticulated cells.*

If we study the *gemmiparous zone* at a stage considerably earlier than that shown in Figure 14, in fact at a stage in which a polypide is about to arise, we find an appearance of the layers represented by Plate I. Fig. 3. In such a region the ectoderm consists of cuboid cells about 7 μ high by 6.5 μ broad. The nuclei are large, nearly spherical, and vary in size from 3.5 μ to 6.0 μ. The largest nuclei are those in the region from which a bud is about to arise (*ex.*). One in this region (to the right of *ex.*) is 6.5 μ by 6.0 μ in diameter, with a nearly spherical, eccentrically placed nucleolus of about 3.0 μ in diameter. This nucleus is the largest which I have found in the whole tissue of Paludicella, and the same is true of the nucleolus. From the examination of many regions from which buds are about to arise, I can assert that such regions always, in Paludicella, possess large nuclei and large deeply staining nucleoli. I shall have occasion to describe similar conditions elsewhere, and to point out the probable significance of these facts. The cell body possesses a highly granular, deeply staining plasma; the inner ends of the cells, however, do not stain so deeply as the middle or peripheral portions.

The cuticula (omitted from Fig. 3, see Fig. 5) is usually somewhat different in appearance from that at the extreme tip. In section we can distinguish two layers: an outer, thicker, deeply staining layer, which is not continuous but appears broken into larger or smaller bits; and an inner, thin, non-stainable and highly refractive portion, from which the first layer is often slightly separated. This second layer is closely applied to the underlying cells, which doubtless secrete it. Looked at from the surface (Fig. 10, *a.*) the deeply stainable layer is seen to be broken into irregular polygonal pieces ranging from 2 μ to 17 μ in diameter and separated from one another by spaces ranging from 0 to 6 μ.

The mesoderm forms a loose epithelium, whose average width is less than that of the ectoderm (Fig. 3, *ms'drm.*). As a whole, moreover, it stains less deeply. In a portion of the gemmiparous zone, which lies about 180° from the budding region, the mesoderm has become so delicate a layer, if it exists at all, as not to be easily distinguishable. In the vicinity of the bud its cells have irregular outlines and extend out into the cœlom as though possessed of the power of amœboid movement. The nuclei are spherical or ovoid, smaller than those of the ectoderm, and on the whole have smaller nucleoli. The cell body is highly vacuolated. The vacuoles are not large and clear in outline, but whole regions of the cell body seem to be reduced to a non-stainable condition, and in some of these regions a fine network may still be observed.

The *proximal zone* (Fig. 14, γ to δ) is distinguished, soon after the first rudiment of the bud appears, by the diminished thickness of the ectoderm. The cells have become transformed from a columnar to a pavement epithelium. The nuclei are smaller, the nucleoli less prominent, and the cell body stains much less deeply. The cuticula is of two kinds, as before, but with this difference: the deeply staining outer part is less conspicuous, and the pieces are smaller and more widely separated. Looked at from the surface, we find an appearance like Figure 10, *c.*, in which the dark bodies represent the deeply staining cuticula. These pieces are much smaller than those of the gemmiparous zone, ranging from 0.6 μ to 9.5 μ in diameter, and separated from each other by spaces ranging from 0 to 13 μ.

3. Origin of the Polypide in the Terminal Bud.

Observation having shown that budding in Paludicella follows definite laws, we ought to be able to discover the place and time at which buds will arise; and it is necessary to do this in order to study the origin of the gemmiparous cells, and the changes which they undergo preparatory to an actual involution.

The study of tips of branches shows that the necks of the polypides of any branch all lie in one plane, and that this plane also includes the youngest polypide; also that the youngest polypides always arise distad of the next older. Knowing these facts, our observations may be confined to a short line running from the neck of the youngest apparent buds to the tips of the branches studied. The time at which to search for incipient buds and the place in the line where they will be found is illustrated by Figure 7 (Plate I.). The youngest *developed* bud is one the axes of whose tentacles are approximately parallel to the axis of the branch, and whose brain cavity, *gn.*, is not yet constricted off from that of the œsophagus. The place of origin is near the tip, immediately beyond the point at which the ectoderm changes rapidly from a columnar to a pavement epithelium.

Figure 3 is from a section across the branch in the region of an incipient bud. I have already described the conditions of the cells of this region. Those near *ex.* are larger than the surrounding ones, and show signs of cell division both in the ectoderm and mesoderm. In both cases shown in the figure, the direction of division is such as will tend to increase the superficial area of the layer in which it occurs. The ectoderm seems to be the most important layer of the two in the process of invagination which is about to take place. I think one is led to this conclusion if one considers a folding of an epithelium to be due to an increase in the area of the epithelium within a certain circumference without a correspondingly great increase in the circumference itself. Such a conception implies, first of all, mutual pressure of the cells of the invaginating epithelium. The cells of the mesodermal layer do not seem to be under mutual pressure; in some cases they are barely in contact. The cells of the ectoderm are evidently closely applied, and probably, therefore, under mutual pressure.

The one case of cell division which is occurring in the ectoderm is at the inner end of the cell. In fact, the centre of the nuclear plate is much nearer the deep end than are the centres of the adjacent nuclei. The effect of this division is to increase the area on the inner surface of the ectoderm more than that on the outer, as appears from a study of the sections shown in Figures 4 and 5. In Figure 4 certain cells lie already below the *niveau* of the surrounding ones, very much as though they had moved downward on account of this being the direction of least resistance. A later stage of this process is shown in Figure 5. Here the nuclei are already arranged in a deep saucer-shaped layer. The transition to the U-shaped arrangement of Figure 37 (Plate IV.), in which the invagination of the inner layer of the bud is completed, is not a difficult one to understand. It is to be observed, however, that the folding is of such character that it can hardly be termed a typical invagination. Comparing Figures 4, 5, and 37, it appears rather to be of a type somewhat intermediate between typical invagination and typical ingression. The cavity of the bud first arises through a rearrangement and reshaping of the cells of the inner layer of the bud. At this stage the nuclei of the invaginated region stain very deeply, and have large nucleoli.

Figure 21 (Plate III.) shows the condition of the bud at this stage as seen in longitudinal section. The proliferation which gave rise to the rudiment of the bud is shown, by a comparison of Figures 37 and 21, not to have been confined to one point, but to have occurred along a line, so that the resulting bud is boat-shaped, and not cup-shaped. The whole mass is therefore bilaterally symmetrical. Even at this early stage one can distinguish a difference in the form of the bud at the anal and oral ends. At the oral end (*Or.*) the bud passes more abruptly into the body wall than at the anal end. Later, this feature becomes more marked. This is an indication of a fact for which later stages will bring better evidence: that the formation of the bud proceeds from the oral towards the anal end, and that the increased length of the bud that one finds in the stage represented by Figure 22 is due to growth at the anal end.

4. ORIGIN AND DEVELOPMENT OF THE LATERAL BRANCHES.

The first lateral branch appears as a prominent protrusion of the lateral walls of an individual of the primary branch when the ganglion of that individual has already nearly closed, and when the bud of the next younger individual has attained a stage somewhat later than that shown in Figure 37. The zone in which the lateral buds arise lies about midway between the neck of the median polypide and the tips of its tentacles at this stage. The place of appearance in this zone is approximately 90° to the right or left of the neck of the polypide of the median individual. In one case measured, however, that shown in Figure 20 (Plate II.), the centres of the two lateral buds seemed to be unequally distant from the neck of the polypide, and each over 90° from it (approximately 100° and 110° respectively. (Compare page 3.)

A cross section of the branch through the region in which the lateral bud is arising shows that the condition of the body wall at the bud is quite different from that of the rest of its extent. Figure 19 represents a longitudinal section of a portion of the body wall passing through the non-budding region. The wall seems to consist of one layer only of cells, and a fine, non-stainable cuticula. This layer of cells is the ectoderm, for it can be traced directly into the outer layer of the tip. The mesodermal layer is not represented in the region from which the figure was drawn, but I believe it is not entirely absent from this part of the individual, for occasionally extremely flattened cells, spindle-shaped in section, may be seen lying inside of the ectodermal layer, quite sharply marked off from it by a distinct line. Further evidence of the existence of two layers is found in the fact that one occasionally sees in the flattened body wall two nuclei lying together, one nearer the cœlom than the other. The cells of the ectoderm are seen to be very much flattened (average 2.5 μ), and their nuclei are widely separated (35 μ). The nuclei are oval, and rather smaller than those near the tip. They possess a single, rather large nucleolus, which does not stain intensely. The cell protoplasm stains very little. The cuticula is about 0.5 μ thick.

If we study the body wall in the budding region, when the latter is first indicated on the surface by a marked protrusion of the outline of the zoœcium (Plate II. Fig. 15), we find that this protrusion is due to an elongation of cells. There are about twenty-two cells in this section, which are more or less thickened. Since the section figured passes through the centre of the circular thickening, and is about one sixteenth the diameter of the circle in thickness, it follows that there are over 250 cells of the ectoderm which have already at this stage become somewhat enlarged previous to evagination. The highest of these cells are the central ones, of which the largest is 22 μ high. The largest nuclei are 4 μ by 6.3 μ, which approximates the size of those in the gemmiparous region (page 6). They are placed nearer the cœlomic epithelium than the exterior, are nearly spherical, and each possesses one large nucleolus and a quite apparent network with deeply stainable nodal points. The cell body is stained as a whole rather deeply by Ehrlich's hæmatoxylin, but particularly around the nuclei. The outer parts of the central cells, however, are stained very little, and the deep ends of some of the lateral cuboid cells not at all. The network of plasma contains only fine granules, and these seem to lie in rows parallel to the long axis of the cell. The structure of the outer-layer cells, at a somewhat earlier stage, is shown in Figure 18, under a higher magnification. The network is very apparent in these large spherical nuclei, and the plasma of the cell is seen to contain coarse granules, which lie near the nuclei and stain deeply.

While the cuticula of Figure 18 is seen to be that of the normal body wall in this region, that shown in Figures 15 and 16 appears under the microscope after staining in hæmatoxylin to be of two distinct kinds: (1) that outside of the central region, which is highly refractive and not at all stained; and (2) that which lies immediately over the central elongated cells of the bud, which is also highly refractive but stains deeply. In fact, the central cuticula resembles in every way that already described for the tip of the branch, and shown in Plate I. Fig. 6. Moreover, it has other points of resemblance to the latter. It does not stain at all in alum cochineal; the outer boundary of the branch is often uneven at this place (Fig. 16); and particles of dirt are often found adhering to it, while the rest of the cuticula is comparatively free. The difference in staining properties of the central and lateral cuticulas indicates that the former undergoes with age a change in its chemical properties; the irregular outer boundary and the adhesion of dirt particles seem to indicate that the newly formed cuticula is viscid. The mesoderm of the stage of Figure 15 consists of a single loose layer of subspherical cells of the two kinds already noticed, reticulated and non-reticulated. The series of Figures 18, 15, and 16 shows the behavior of columnar cells in the formation of a typical outfolding as distinguished from the slipping in of cells to form the polypide (Figs. 3, 4, and 5).

In stages later than that of Figure 16, the tip of the branch becomes further removed from the body wall of the median branch. The cells at the tip always retain their elongated columnar condition. A polypide is soon formed on the upper part of the body wall immediately behind the tip, exactly as in the case of the median branch. A septum is very early formed, cutting off the lateral from the median individual, and the lateral secondary branch becomes the median primary one of new individuals (Plate VI. Fig. 58).

We have already traced out the origin of the polypide of the median branch from the mass of cuboidal cells near the tip; it remains to determine whether the cells which give rise to the lateral branch can be traced directly back to the cuboidal cells of the tip, or whether they have arisen from the flattened epithelium of the general body wall and secondarily acquired their plump "embryonic" character.

Figure 18 (Plate II.), to the cellular conditions of which I have already referred, shows an early stage of the lateral branch, and Figure 20, *gm. l.*, shows on a smaller scale the different cellular conditions in the body wall in the region of two lateral buds which are yet far from showing external signs of evagination. The cells are cuboid and much higher than those of the adjacent body wall. Have they been so ever since they were derived from the tip, or have they secondarily become so ? I believe that these cells have never been flattened pavement epithelial cells, for the following reason. All ectodermal cells of the body wall near the tip are cuboidal; if these cells have only secondarily acquired this form, they must have passed through a stage in which they were flattened epithelium. Now, if these cells could be distinguished by greater thickness from the cells of the surrounding body wall, at a time at which the latter cells had only just begun to emerge from the cuboidal condition to become differentiated into the pavement epithelium of the body wall, it would follow that, even though they had secondarily increased in size as a result of an impulse preparatory to evagination, and even though they would have been at a stage only a very little earlier indistinguishable from the other cells of the body wall, yet they would never have passed in this case through a flattened condition, because at a stage only a very little earlier the whole body wall was composed of cuboid cells.

The conditions which I have set as the criterion of our problem are fairly realized in Figure 17, which represents a portion of the body wall of a median branch which extends from the gemmiparous region above to the thickened body wall of the nascent lateral bud below (*gm. l.*). It will be seen, by a comparison of the body wall of this region with that shown in Figure 19, which is taken from the same individual farther from the tip, that even the most differentiated part of the body wall of Figure 17 is in a relatively indifferent condition as compared with the pavement epithelium of the ectoderm of Figure 19, in which the mesoderm, indeed, has become so thin and insignificant as scarcely to be visible. We may, therefore, maintain that the ectodermic cells of the body wall have only just begun to lose their cuboidal condition to become pavement epithelium, and therefore conclude, in accordance with the argument just presented, that the cells of the lateral bud (*gm. l.*) have never passed through a stage in which they were flattened epithelium. It is evident, also, that the *Anlage* of the second lateral bud is also derived from near the tip, because, as in Figure 20, we find two lateral regions of cuboidal cells.

5. Development of the Body Wall.

It is, of course, almost impossible to gain direct evidence upon the place of origin and method of development of the body wall, and one is therefore forced to the collection and weighing of circumstantial evidence. Braem ('90, pp. 127, 128, 131) believes that the body wall (the cystid, in Nitsche's sense) has a double origin in Paludicella: "Ein Theil des Cystids zwar vor dem Polypid, ein anderer aber erst später angelegt und zwar aus der polypoiden Knospe selbst entwickelt wird." The part developed from the bud of the polypide is the elliptical region of the body wall, whose main axis lies in the sagittal plane and which has the neck of the polypide at the distal focus and the attached ends of the retractor muscles and the parietovaginal (or pyramidal) muscles lying in the proximal circumference, — the greatest part of the ellipse thus lying oral of the atrial opening. The evidence for this conclusion Braem finds in the following facts, which my own observations confirm: "The great retractor first appears in the angle between the oral part of the polypide bud and the cystid wall [cf. Figs. 23, 24, *cl. mu. ret.*]; then its cells gradually become elongated, and as its point of origin retreats farther and farther from the polypide, it finally appears as a bundle which joins a point lying between the mouth of the polypide [neck of the polypide] and the inferior septum with the pharynx, and, as I believe, also with the cardial part of the stomach" (p. 125). Compare the muscles at the left end of Plate I. Fig. 8. Further on he says: "Die Parietovaginalmuskeln [pyramidal muscles] erscheinen an der Knospe zuerst in Form zweier seitlichen Leisten, in welchen die einzelnen jugendlichen Fasern senkrecht zur Längsaxe verlaufen. Indem sich alsdann lateral von der Knospe das Cystid durch Neubildungen erweitert, werden die Fasern verlängert und die beiden Bündel treten in Flügelform deutlicher zur Rechten und Linken der Mündung hervor. Ihr Ursprung an der Cystidwand rückt nun von der Mündung immer weiter ab und gelangt schliesslich auf die gegenüberliegende Seite, wo er anal und lateral seinen definitiven Platz findet." Compare Plate I. Figs. 7–9, *mu. pyr.*, and Plate VI. Fig. 63, *mu. pyr.* From these observations Braem ('90, pp. 127, 128) concludes: "So scheint es sicher, dass auch hier ein grosser Theil des definitiven Cystids, das ja zum anderen Theil schon vor der polypiden Knospenanlage entwickelt war, aus dem Material dieser letzteren hervorgeht. Das folgt namentlich aus der Art und Weise, wie sich die Muskeln bilden. . . . Auch hier würde, wie bei den Phylactolæmen, oral vor der Knospe nach dem Retractor hin, ein grösseres Gebiet der Leibeswand der Knospenanlage entstammen, als seitwärts und hinten."

An analysis of the facts has led me to conclusions differing somewhat from those of Braem; namely, that all or nearly all of the cells of the body wall (cystid) are derived from the tip of the branch or from the immediate descendants of cells so derived. The number of cells contributed to the formation of the body wall by the neck of the polypide is much smaller than Braem has suggested, and probably insignificant in amount. The retreat of the points of origin of the retractor and parietovaginal (pyramidal) muscles may be in part accounted for by the normal growth in area of the body wall, and in part by the actual movement of the point of origin with reference to the cells of the body wall. These conclusions rest upon the following circumstantial evidence.

Owing to the small number of cells in the body wall at the tip, and the comparatively slow growth of the cystid, karyokinetic figures are much less frequent than in the polypide. Quite a long search has therefore not afforded cases enough to enable me to draw any perfectly satisfactory conclusions as to just where, and where only, growth was taking place. I have, however, seen nuclear division occurring in the elongated cells of the extreme tip, rather more abundantly in the cuboidal cells between the extreme tip and the gemmiparous zone, and most abundantly in the gemmiparous zone, but here evidently having to do with the origin of the polypide, muscle cells, etc. Proximal to the gemmiparous zone, I have noted few cases of nuclear division excepting about the neck of the polypide. It seems probable that the cells of the tip of the branch are not to be regarded as forming a differentiated organ whose elements rarely divide, but as quite capable of adding new cells to the body wall. On the other hand, there is by no means a *Scheitel* in the botanical sense, but the cells added to the body wall continue for a time to divide vigorously, and finally give rise to the polypide, to the *Anlage* of the lateral branches, and to the body wall. The cells belonging to the proper cystid then cease to divide rapidly.

I have already shown how the cells of the tip secrete a cuticula, which becomes gradually replaced by a second cuticula secreted beneath it as the body wall attains its adult dimensions. It appears as though the first cuticula were secreted by the cells of the tip *only*. This being so, since the area of the body wall increases, this first cuticula must either stretch to cover the enlarged area, or else it will fail to cover it and appear as isolated patches upon the body wall, and these isolated patches will become more and more widely separated as the area of the body wall increases. This latter condition seems to be the one realized in this case. The presence of the old cuticula is easy to demonstrate, since it stains deeply in hæmatoxylin; and it may be easily distinguished from that formed later, for with the same reagent this stains not at all. Figures 6, 11, 12, and 13 show different appearances of the cuticula at different parts of the body wall. At the extreme tip (Fig. 6) there is a continuous deeply stained band of cuticula. In Figure 11 it no longer appears quite homogeneous, but is darker at some places than at others. The ectoderm is here composed of cuboidal cells. At a later stage of development the ectodermal cells have become very much flattened. A thin, unstainable, more deeply lying cuticula has already begun to form, and the outer deeply stainable cuticula is seen to be broken up into bits. Figure 13 is from the adult body wall. The ectoderm is flattened. The inner cuticula has attained a great thickness, and the outer cuticula is represented by only a few deeply staining patches. One attains a similar result by studying the surface of a stained individual. Figure 10 shows the condition of the outer cuticula at intervals along the same branch from the gemmiparous region *a* to a nearly adult region, *d*. The bits of cuticula become more and more widely separated and smaller, as I have already described in detail on page 7. Here, then, we have not merely an interesting case of replacement of one cuticula by another to meet the needs of the enlarged body wall by a method which has no parallel, so far as I know, in any other group of animals, but for the specific purposes of our problem *a criterion of growth of the body wall* quite as satisfactory as karyokinesis, and much easier of application.

Let us apply this criterion in our attempt to answer the question, Is that portion of the body wall lying between the neck of the polypide and the points of origin of the pyramidal muscles (Plate VI. Fig. 63, *b–a*, *b–c*) derived wholly from the neck, or is it merely the result of interstitial growth of that part of the original cystid which was preformed in the neck region? If the first condition is true, we should expect to find no indications of the outer cuticula secreted by the tip of the branch; if the second, we should expect to find the outer cuticula broken into bits, and underlaid by the inner lately formed cuticula. Figure 63 shows clearly the deeply stained outer cuticula here separated into bits, and, to my mind, thereby proves that this part of the cystid has had an origin similar to that of the rest of the body wall. Moreover, a comparison of the portion of the section figured with the remainder (and this comparison has been made on many sections from several individuals) shows that the parts of the cuticula about the neck are indeed rather smaller and farther removed from each other than at the opposite side of the branch; but the difference in this respect is not very marked, and may well only signify that there is a more rapid growth of the body wall in the vicinity of the neck of the polypide than at the opposite side.

But how then do the points of origin of the pyramidal muscles come gradually to move away from the neck of the polypide at which they arose, in order finally to lie so that the muscle fibres are nearly parallel? If the points of origin remain fixed with reference to the surrounding cells, they can hardly come to lie *absolutely* closer together, but only *relatively* so by growth of the body wall between these points and the neck. If, however, we find that in older individuals the points of origin are not only relatively but absolutely closer together, we are driven to the conclusion that these points move relatively to the surrounding cells. To decide whether the points of origin come to lie closer together behind the neck *absolutely* or only *relatively*, I measured cross sections of four individuals through the region of the neck in which the muscle fibres showed evident differences of length, and therefore of age. I may preface a table of these measurements with the statement that the muscles first appear plainly differentiated at a stage when the polypide is well formed (Fig. 7, *mu. pyr.*), and that the growth of the body wall in circumference is not very considerable after this time. The numbers indicate measurements in micra: —

	No. 1.	No. 2.	No. 3.	No. 4.
Distance on periphery between origins of muscles, atrial side	150	154	187	260
Distance on periphery between origins of muscles, abatrial side	297	286	264	220
Total length of periphery	447	440	451	480

The distance on the "atrial side" signifies the distance measured over *a*, *b*, *c*, Figure 63 (Plate VI.). The length of the remainder of the section is the distance on the "abatrial side."

From these measurements it appears that the "origins" of the pyramidal muscles approach each other absolutely, — a condition which Braem's hypothesis cannot explain, and which can be reasonably interpreted, it seems to me, only by assuming, however unique and difficult of conception such a condition may be, that the points of origin move relatively to the surrounding cells of the body wall. (Compare also the movement of parietal muscles referred to on page 29.[1])

It is not necessary to assume that the increase in extent of the body wall after the polypide is first formed is due to the addition of cells from the neck. The change in form of the ectodermic cells from a columnar to a pavement epithelium must alone cause a great increase in the extent of that layer. Some measurements that I have made seem to me to prove that the area of the body wall does increase greatly, even outside the region whose growth Braem attributed to the addition of cells from the neck of the polypide. Thus, in one case, the distance from the distal end of the polypide bud, which becomes the neck of the adult, to the point of origin of the young retractor muscle was 0.17 mm.; from the same point to the septum separating the young individual from the next older was 0.27 mm. In the next older individual, from the neck to the origin of the retractor muscle was 0.72 mm.; from the neck to the septum was 2.0 mm. Thus assuming that the older individual passed through a stage exactly equivalent to that in which we find the younger, the distance from the neck to the origin of the retractors has increased 0.55 mm., and from the origin of the retractors to the septum 1.18 mm. The first distance is that in which Braem has assumed the body wall to grow by additions from the neck of the polypide, and this assumption was apparently made to account for the increase in extent of this region; but the area between the origin of the retractors and the septum, which is outside the region to which additions such as Braem contemplates could have been made, has grown in this case very considerably more in extent. This case is not a typical one, however, for we rarely find the distance from the origin of the retractor to the septum to be so great. In general, from observation of a number of cases, I should say that in the adult the distance between the neck of the polypide and the origin of the retractors, is to the distance between the latter and the septum about as 5 : 4, and that therefore the growth of the first region is slightly greater than that of the second. From the fact, however, that the cells around the neck of the polypide for a long time retain a somewhat embryonic character, and may quite frequently be seen in division, this was to have been expected. The conclusion which I draw from this last series of conditions is, then, that it is unnecessary to suppose the addition of cells from the neck of the polypide to account for the fact that the origin of the retractors is carried backward from the polypide. Normal growth of the body wall, such as occurs elsewhere, is quite sufficient to account for it.

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[1] Professor Mark has called my attention to a discussion of the movement of the fixation-point of a muscle in Mollusks by Tullberg ('82, pp. 26, 27, 44). This author says that he has undertaken no special investigation of the method of migration, but concludes that this motion must result from the absorption of the inner muscle fibres as new ones are formed on the outside. I do not find any evidence of such a process in Paludicella.

To recapitulate. That portion of the cystid lying in the vicinity of the neck can hardly be derived from the neck alone, for the cells still show adhering to them the cuticula which they derived from the tip of the branch. It is not necessary, in order to account for the movement of the origins of the muscles away from the neck, to suppose that the circumcervical region is derived in that way; for (1) the origins of the pyramidal muscles actively migrate away from the neck to a certain extent, and (2) the normal growth of the body wall is sufficient to account for the carrying backward of the origin of the retractors.

From the facts already gained it seems clear that the ectocyst (cuticula) is first formed at the tip, and then, to meet the wants of the growing colony, this is replaced later by a cuticula of different chemical composition, which becomes thicker as the body wall grows older. At a late stage we find a separation of the thick cuticula itself into two layers, of which the outer one is much the more highly refractive.[1] (Plate II. Fig. 13; Plate III. Figs. 26, 29.)

6. Development of the Polypide.

We have already (pages 8, 9, Figs. 5, 14, 37) seen how the foundations of the polypide are laid by the ingression of cells of the outer layer of the body wall pushing before them the mesoderm, and how, finally, those cells arrange themselves in a boat-shaped mass to form the inner layer of the bud (Plate III. Fig. 21), which possesses no actual cavity, and is constantly separated from the external world by the ectoderm which remains behind to form the neck of the polypide. Even when a cavity is formed later, it does not communicate with the exterior until the permanent atrial opening has arisen. The earliest differentiation in the bud is, as mentioned by Allmann ('56, p. 36), the formation of a cavity which is to become that of the atrium. This cavity is first formed at an early stage as an extremely slight fissure in the midst of the inner layer. Figure 22 shows a longitudinal section of this stage. Cell division is taking place throughout the whole mass, but especially at the neck of the polypide, *cev. pyd.* The position of the cavity is represented by the central non-nucleated space, and this gives rise, as the later history of development shows, to the atrium and the pharynx.

Figure 23 represents a stage which is doubtless of short duration, for I have found it only twice. The bud is much more developed at the anal end than in the last stage, and there is a second cavity below the atrium, from which it is separated by a line of nuclei. This is plainly an early stage in the formation of the *alimentary tract*, which thus first appears at the anal side of the bud, as in Phylactolæmata, and is progressively formed towards the oral end. An appearance similar to the one figured would be given by a slightly oblique section of a later stage; but this section is strictly sagittal, and no trace of the lumen appears in adjacent sections. I have found a similar condition in a series of longitudinal sections at right angles to the sagittal plane of the bud (Plate IV. Figs. 39 and 40). Figure 39 shows that the atrio-pharyngeal cavity is first developed at the anal end, and in Figure 40, which is three sections (about 15 μ) below Figure 39, the anal end only of the alimentary tract is formed. It is worthy of notice that the cells of the mesodermic layer of the bud are often greatly vacuolated at this stage, as in Figures 39 and 40, *vac.* Braem ('90, p. 126) says of this stage: "Die der Resorption dienenden Darmabschnitte, Magen und Enddarm, werden gemeinsam angelegt, indem auf jeder Seite der Knospe eine Längsfalte die Wandungen nach innen und gegen einander zu einbiegt, worauf die benachbarten Theile des inneren Blattes verschmelzen und so durch eine Art Abschnürung das primäre Knospenlumen in den vorderen Atrialraum und die hintere Darmhöhle getrennt wird." While I thoroughly agree with this statement, the additional fact of the formation of the tract *progressing from the anal towards the oral end* is interesting, in that it shows that the process of formation of the organ in Paludicella is fundamentally similar to, although differing slightly in detail from, that of the Phylactolæmata. Figure 24 shows in sagittal section a still later stage in the development of the alimentary tract. A cross section of this stage is seen in Figure 30 (Plate IV.), in which the separation of atrial and gastric cavities is demonstrated. The inner layer of the bud is here seen to be separated from the ectoderm by a distinct line, and, to a certain extent, even by the mesoderm. The distal (oral) part of the cavity of the alimentary tract next becomes considerably enlarged to form the stomach (Fig. 25). The outer layer of the bud, *ms'drm.*, penetrates between the stomach and the atrium, and a depression is formed at the bottom of the atrial chamber which will give rise to the œsophagus. Even at this stage the œsophagus is not in communication with the stomach, but their cavities are separated by two layers of cells of the inner layer of the bud. These two layers become those of the cardiac valve (Plate IV. Fig. 36, *vlv. cr.*). By a further comparison of Figures 25 and 36 it will be noticed that, whereas in the earlier stage, as in Endoprocta, there is no cœcum to the alimentary tract, in the later stage the cœcum has already begun to form, as in Phylactolæmata, by an outpocketing of nearly the whole of the lower wall of the stomach. (Compare also Plate I. Figs. 7, 8, and 9.)

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[1] Such a two-layered condition of the cuticula was long ago described by Reichert ('70, pp. 265, 266) for Zoöbotryon. He distinguished "eine *äussere, festere,* stärker lichtbrechende und sprödere Schicht und die *innere weichere.*" Realizing that the "ectocyst" or cuticula undergoes many changes in form, — formation of lateral buds, of septæ or communication plates, and increase in size of the stolon, — he suggested, without having observed the process, that probably during these changes the more rigid outer layer disappeared and was replaced by the inner softer one.

Very soon after the establishment of the alimentary tract, and between the stages shown in Figures 24 and 25 in sagittal section, there begin to appear organs which have a very considerable phylogenetic significance; namely, the lophophoric ridges, ring canal, and tentacles.

The *lophophoric ridge* is a fold which surrounds the mouth, and from which at intervals tentacles arise. The ridge, however, arises before the tentacles. The general position of the ridge, as well as its method of origin, may be learned from an inspection of a series of sections of the age of those shown in Figures 31–34. In a section lying near the oral end of the bud (Fig. 33), one finds two spaces, — a lower, which is that of the stomach, and an upper, the œsophagus and atrium. This upper space is broader above than below, and the cell layer which lines it is thick below, but above, or nearer to the body wall of the budding individual, it is thinner. The transition from one condition to the other is quite abrupt, and is marked by a salient curve (*loph.*). In a section near the anal end of the bud (Fig. 31), it will be seen that here too the inner layer is thick below and thin above. The characters mentioned are still more strikingly shown in the median section, Figure 32. That the differences in thickness of different parts of the inner layer are recently acquired modifications of an earlier simpler condition is indicated by comparing Figure 32 with Figure 30, which is from a younger bud. The series of points (*loph.*) of transition from thick to thin epithelium forms on the reconstructed polypide a curved line, convex above. This line is the ridge of the young lophophore (compare Fig. 25, *loph.*). I have said that the lophophoric ridge arises before the tentacles. The evidence for this assertion is found in a series like that referred to above, where, although the ridge exists along the entire side of the atrium, one finds nascent tentacles in the middle region only (Figure 32, left hand).

As Figure 25, of a later stage than Figures 31–33, shows, the lophophore curves downwards rapidly at the anal end, so that it here lies at right angles to the axis of the rectum, but does not extend at all beyond the anus. Orally, there is in the median plane only the slightest trace of the lophophoric ridge. By the formation of this ridge in the wall on each side of the atrial chamber, the original atrio-pharyngeal cavity has become separated into two regions. The space lying within or below the ridge forms the pharynx and the intertentacular space; that lying without and above, the atrium of the adult. (Plate III. Fig. 25; Plate IV. Fig. 32, *atr.*) Since the lophophore curves rapidly downward to the anus and does not extend behind it, the act of cutting off the lower part of the atrio-pharyngeal cavity from the upper (atrium proper) does not continue behind the anus, which therefore opens directly into a part of the atrium. This part has the form of a compressed funnel, and is bounded behind and laterally by the kamptoderm, and orally by the hinder ends of the lophophoric ridges, and also, since the latter do not meet in the median plane, by the pharyngeal cavity. Thus it has come about that the anus, which at first opened into the common atrio-pharyngeal cavity of the bud, has now, in the separation of the two regions, come to lie near their point of division posteriorly, but to open distinctly into the atrial cavity. The more pronounced separation of the part of the atrial cavity into which the anus directly opens from the remainder of the atrium takes place much later, and will be described further on.

In Figure 33, the *ring canal* (*can. crc.*) is seen to be already formed. At this stage it is found on one side only, the left, if one looks at the polypide from the tip of the branch. It occurs in only four sections (each 5 μ thick), being found on the next section behind Figure 33, and on two sections nearer the oral end. At its oral extremity, it terminates blindly as a thickening of the outer layer of the bud; at its anal end, one sees cells of the outer layer extending out partly over the canal, but failing to enclose it; in the next section the mesoderm is undisturbed. In similar sections of an older polypide (corresponding in age approximately to Plate IV. Fig. 35), the canal is found on both sides, and near to the oral end, but at about the middle of the series (cf. Fig. 35) it is found to open again into the body cavity. I therefore conclude that the ring canal makes its first appearance at the base of the lophophore in a region just oral of the middle of the polypide. Exactly how it arises, whether by a growing together of the lips of a shallow furrow formed from the mesodermal layer, or by the formation of a pocket, which, elongating, penetrates between the inner and outer layers of the polypide at the base of the nascent lophophore, I have not been able to determine. Two facts induce me to believe that the later formation of the canal oralwards results from the penetration of a sac-like mass of mesodermal cells between the two layers of the polypide at the base of the nascent lophophore. One usually finds, (1) as in Figure 33, *can. crc.*, a double mesodermal wall between the lumen of the canal and the cœlom, and one layer between the former and the inner layer of the bud; and (2) at the oral blind end of the ring canal a number of loose cells (occasionally dividing) representing the blind end of the pocket and lying between the inner and outer layers, both of which are intact.

Braem ('90, p. 50) describes the formation of the ring canal in Phylactolæmata as taking place in the manner just suggested for Paludicella. His studies were made, he says, preferably on statoblast animals. Nitsche ('75, p. 358) concluded that in Phylactolæmata the ring canal was first a furrow, whose lips fused, and my own study ('90, p. 129) has led me to the same conclusion. Since reading Braem's account I have looked over some of my own sections of Cristatella again. Certainly the process is not so clear in the buds of the adult colony as in the statoblast embryo which Braem figures. Nevertheless the series of sections ('90, Plate IV. Figs. 33–38) given as evidence of my statement still seem to me capable only of the conclusion I drew from them. Perhaps the processes may be different in detail in the two cases; certainly the two explanations are not fundamentally dissimilar.

The ring canal being established in the oral part of the polypide, it grows forward, as I have said, and, secondarily, the canals of both sides meet in the median oral line and their lumina become confluent (Plate VI. Fig. 52, *can. crc.*). From what has already been said, it is clear that the lateral parts of the ring canal are not now continuous with each other behind. They become so only after the formation of the tentacles.

The *tentacles* arise upon the lophophoric ridge at a stage a little later than that represented in Plate IV. Figure 32. At the stage represented by Figure 35, however, the tentacles have begun to form, as indicated by the fact that in the series from which this figure was taken the fold into the upper part of the atrium appears now deep, now shallow, according as the section passes through the length of a young tentacle, or only through the lophophoric ridge between the tentacles. The position of the section (Fig. 35) is about the middle of the series, corresponding to Figure 32.

By a comparison of Figure 35 with Figure 32 in respect to the tentacles, it will be apparent, first of all, that the lophophoric ridge itself has been heightened and that this heightening has been effected, not by a deepening of the fold existing in Figure 32, the lips of the fold remaining quiescent, but by a movement downwards of the outer lip (*) of the groove which is to form the ring canal. The movement is of course accompanied by an increase in the length of the kamptoderm, *kmp. drm.* This growth of the lophophoric ridge naturally does not result in making the tentacles project farther above the ridge. Their elongation must take place quite independently of the former's. The lophophoric ridges have now become elongated folds lying upon the right and left of the polypide, which at this stage has a very compressed appearance (Plate IV. Fig. 41). The folds occupy the position of the ridges, and therefore do not lie throughout their whole extent in one plane, but oralwards are nearly parallel to the body wall (Plate III. Fig. 25), analwards trend nearly at right angles to it. It results from this fact, that one cannot see the anal tentacles when looking at the polypide from the side of the body wall to which it is attached. Figure 41 (Plate IV.) shows also that no tentacles have yet made their appearance at the oral ends of the two lophophoric ridges.[1] The tentacles are here seen to be arising in two long rows, and so that those of one row are placed opposite the intertentacular spaces of the other. There are six tentacles in each row. The rows are not continuous with each other oralwards or analwards.

The separation of the atrial and oral cavities, begun by the first formation of the lophophore, is, now that the tentacles have arisen, much more pronounced. Other changes now occur in this region, which produce an extensive modification in the form of the polypide.

One of the first of these changes is the close approximation and finally fusion of the anal extremities of the lophophoric ridges oralward of the anus. A stage in this is shown in Figures 43 and 44 (Plate V.), which are sections in the position of the lines *43*, *44*, of Figure 25 (Plate III.), but through a slightly older polypide than that represented by Figure 25. The section shown in Figure 43 passes across the rectum, grazes the outer lip of the ring groove of the anal tentacles, and finally cuts, nearly longitudinally, one of the middle tentacles of the row. The two lophophores are not yet completely fused in front of the rectum. In Figure 44 (compare Plate III. Fig. 25, *44*) this break in the continuity of the lophophore is more prominent.

By the completion of the union of the lophophores in front of the anus, the rectum is quite cut off from communication with the intertacular space. It now opens only into the thin-walled, funnel-shaped depression of the atrial cavity.

Pari passu with this operation the stomach and rectum are being more completely separated from the pharyngeal cavity by the penetration of a double layer of mesoderm between these regions from each side, and a fusion of the corresponding layers of the two sides. Finally, the walls of the stomach and pharynx become separated from each other by a part of the cœlomic cavity, as in Plate IV. Figure 36. This process of separation of the alimentary tract proceeds analwards, and finally the rectum is far removed from the œsophagus.

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[1] Compare Plate IX. Figure 77, which is a superficial view of the young lophophore from Flustrella, in which the process is similar to that in Paludicella, only the down curving of the anal tentacles occurs later than in the latter case.

The anus thus comes to lie farther outside of the anal tentacles. Finally, the ring canal, which is formed progressively farther and farther analwards, follows the fusion of the anal ends of the lophophores, and thus completes the canal behind the œsophagus. (Plate IV. Fig. 36; Plate VI. Fig. 53, *can. crc.*)

The anal part of the ring canal is doubtless not merely a groove, but a tube; but the ring canal is not closed at this, and probably not at any stage throughout its entire extent, for in Plate VI. Figure 52, two sections below Figure 53, an opening is shown to exist on each side (at *can. crc.*), putting the cavities of the ring canals and the cœlom into communication with each other. These openings lie at the sides of and slightly above the ganglion (*gn.*, Fig. 52); a position exactly comparable with that of the openings in the ring canal of Phylactolæmata, which leads from the cœlom into the lophophoric arms on the one hand, and into the circumoral part of the ring canal on the other.

By a comparison of Figure 41 (Plate IV.) with the sections shown in Figures 60–62, it will be seen that the row of tentacles has undergone a change of form: from being laterally compressed, it has become circular. This change of form has not resulted from an increase in the number of the tentacles, for at the stage of Figure 41 there are six tentacles on each side already formed (the sixth not visible), and there are in front of the mouth spaces already reserved for the two additional tentacles. There are also, probably, two nascent tentacles at the anus, although these are little developed, making a total of 16. In Figure 61 there are only 15 tentacles; moreover, the actual diameter of the tentacular corona in the sagittal plane is less than at the earlier stage of Figure 41. This change of form is perfectly normal, all young polypides having tentacles arranged in two parallel rows, and adult polypides having a circular lophophore.

These changes in the form of the tentacular corona are correlated with important changes in the direction of the axes of other organs. These changes may be understood by comparison of Figures 25 and 36, together with the assistance of Figures 7–9, all of which are oriented in the same manner. In Figure 25 the points fixed by the cardiac valve (*vlv. cr.*) and anus (*an.*) lie in a line which is approximately parallel to the body wall. In Figure 36 the line passing through the same points makes an evident, but not very large, angle with the body wall. This line has undergone, then, a slight change of position only. The axis of the anal tentacles lies in both cases nearly parallel to the body wall, and so does the neural wall of the pharynx. The oral tentacles, on the contrary, whose axes in the earlier stage are directed perpendicularly to the body wall, lie in the later stage with their axes parallel to the wall; and the base of the lophophore, which in the earlier stage trended at its oral end parallel, at its anal perpendicular to the body wall, in the later lies throughout its whole extent in one plane perpendicular to the body wall. The axes of the oral tentacles have rotated through an angle of nearly 90° relatively to most of the other organs of the polypide. The cause of this rotation must evidently be sought in unequal growth in different parts of the polypide. A comparison of the length of the kamptoderm on the anal side in Figures 25 and 7 indicates that it has grown more in length than on the oral side. This excessive growth would tend to rotate the line *vlv. cr.* — *an.* to a position perpendicular to the body wall. Since this rotation has not occurred to so great an extent as was to have been expected, we must look for a compensating growth on the oral side of the polypide, between *vlv. cr.* and the neck of the polypide, which shall be nearly equal to the excessive growth of the anal kamptoderm, and which must be *outside* of the oral kamptodem. These conditions of location are fulfilled only by the oral wall of the œsophagus, and it is by change of position and growth of this wall that the extension of the anal kamptoderm is nearly compensated for on the oral side of the polypide. By this growth in the wall of the œsophagus the oral part of the ring canal has been brought to lie over the anal part, the sagittal diameter of the tentacular corona has been reduced, and the compressed lophophore has been transformed into a circular one.

Concerning the number of tentacles, Dumortier et van Beneden ('50, p. 46) observe that in the adult there are ordinarily 16, although individuals with 18 tentacles occur not infrequently, an observation which Kraepelin ('87, pp. 98, 99) confirms. In addition to these numbers, I have found 15 and 17. The growth of the odd tentacle is quite interesting. The sections reproduced in Figures 60–62 (Plate VI.) will serve to illustrate a condition which I have quite frequently found in a polypide with 17 tentacles. In this particular series there are only 15 tentacles. The successive sections abundantly demonstrate that the odd tentacle (*) is anal in position, and that it is younger than any of the others; thus in Figure 61 its tip is cut, in Figure 60 there are only 14 tentacles visible, and these are found in the two following sections. Since there are six sections which pass through the tentacles, and the odd tentacle is found in only three of these, it follows that it is only about one half as long as the others.

The *nervous system* arises, as in Phylactolæmata, by a depression in the floor of the common atrio-pharyngeal cavity, in the region which later becomes the anal surface of the pharynx. As in Phylactolæmata, we first see a shallow pit (Fig. 25, *gn.*). This appears to become deeper, sinking downward and somewhat toward the cardiac valve (Fig. 78, *gn.*). Finally it becomes constricted off from the wall of the œsophagus, and then appears as a cellular mass closely attached to it and surrounded exteriorly only by mesoderm. (Plate I. Fig. 8; Plate VI. Figs. 52, 53, *gn.*) Even before the closure of the ganglionic pocket is completed, the formation of the circumœsophageal nerve, first described by Kraepelin ('87, pp. 62, 63) in the adult, begins.

Figure 52 (Plate VI.) shows a transverse section of a young polypide in which the ganglion is solid, and not provided with a large cavity as in Phylactolæmata. There is a small cavity in the upper part of the ganglion, and this is not yet wholly closed from the œsophagus. The ganglion is continuous with a pair of hornlike processes (*n.*) which partly enclose the œsophagus, and at a later stage do so wholly (Plate IV. Fig. 36, *n'.*) The cells of these horns are found dividing in unusual abundance. The horns lie next to the digestive epithelium, and between it and the mesodermal lining of the ring canal. From the method of growth, and from the sharp line of separation between the tips of the horns and the surrounding tissue, there can be little doubt that the circumœsophageal nerve of Paludicella, like the lophophoric nerves of Phylactolæmata, arises as an outgrowth of the brain.

Serial sections show that the ganglion suddenly diminishes in size immediately below the point at which the circumoral nerves arise, but one can trace a layer of cells continuous with the brain downwards for ten or fifteen micra farther, to near the cardiac valve. At this point one can still see nuclei of a third layer lying between the digestive epithelium of the valve and the mesoderm. It seems to me, therefore, that this may be regarded as a gastric nerve, which seems to originate by a single root and later to give rise to two nerves, one of which lies on either side of the cardiac valve.

7. Origin of the Muscles.

a. Retractor. — After its first formation the bud becomes elongated in the direction of the axis of the branch. The derivation of this elongated stage from the much shorter earlier one might be effected in one of two ways: either, first, by the ingression of cells from the ectoderm at points successively more and more remote from the point of primary invagination, the additions to the length of the bud being made by a continuation backwards of that process by which the first foundations were laid; or secondly, by cell proliferation at the point of first invagination pushing the oral end of the buds farther and farther from the neck of the polypide.

I think there can be little doubt that the second is the method by which the bud becomes elongated; and for the following reasons. (1) The oral end of the bud, on the supposition of continued invagination of the body wall, should become very gradually of less diameter, and transverse sections at that end should exhibit the ingression (potential invagination) of cells which were observed in the earliest stage; but as a matter of fact the oral end is abrupt (Plate III. Fig. 22, 23, *Or.*), and no stages of ingression are to be found there. (2) On the first assumption, the inner layer of the bud should be at all points in equally close relation to the ectoderm of the body wall; on the second, the inner layer should be closely connected with the ectoderm at the neck of the polypide (Plate III. Fig. 22, *cev. pyd.*), but elsewhere it should be sharply separated from it. As a matter of fact, a sharp line can be distinguished, in a sagittal section, separating the inner layer of the bud from the overlying ectoderm at all points except at the neck (anal part) of the polypide (Plate III. Figs. 22–25). Moreover, cross sections of the anal part of the bud show the inner layer passing directly into the ectoderm, and oralward the outer layer of the bud tends to penetrate more and more between the ectoderm and the inner layer. Therefore I conclude that the inner layer of the bud is constantly augmented by cell proliferation in its mass, and especially at the neck of the polypide, and this explanation also accounts for the active cell proliferation observed at the neck in Plate III. Figure 22, *cev. pyd.*

Since the polypide later becomes attached to the body wall by the comparatively narrow "neck" only (Figs. 7, 9, *cev. pyd.*), a separation of the oral part from the body wall has to take place. This process begins at the oral end. In its earliest stages it is indicated by the sharp separation of the inner bud-layer from the overlying ectoderm, and the partial penetration of the mesoderm on each side into the space between these two layers (Plate IV. Fig. 30, *ms'drm.*). At a later stage the mesoderm may be seen as a single cell layer lying between the ectoderm and the inner layer of the bud midway between the oral and anal ends (Plate IV. Fig. 32, *ms'drm.*), and as a double cell layer at the oral end of the bud (Fig. 34, *ms'drm.*). It is from these cells at the oral end of the bud that the retractor muscles are to arise (Plate III. Figs. 23–25, *cl. mu. ret.*). As the oral end of the kamptoderm and œsophagus to which their inner ends are attached moves away from the ectoderm, and as the area of the latter itself increases, the two ends of the cells move farther and farther apart, and the young muscle cells become drawn out into spindle-shaped muscle fibres. (Plate III. Fig. 25, *cl. mu. ret.*; Plate IV. Fig. 36, *mu. ret.*) The retractor thus arises unpaired and remains so at its origin, but nearer its insertion in the ring canal and œsophagus one can distinguish a division into right and left masses. The adult muscle fibres consist of two parts at least, the inner contractile portion and an outer less modified protoplasmic portion, which can be traced over the whole of the first part, but is most evident around the nucleus, where it has a granular appearance.

b. Pyramidalis. — At about the stage of Figure 25 (Plate III.) one finds, on cross sections of the branch which pass through the neck of the polypide, that the mesoderm of the body wall on each side of the neck is greatly thickened, and that its closely packed cells, which lie three or four deep, have become somewhat elongated. Cell division is quite common in the ectoderm of this region, and by it the area of the circumcervical region is increased and the two ends of the muscle fibres are carried farther apart, one end remaining attached to the neck of the polypide and the other moving towards the abatrial surface. I have given reasons above (page 16) for believing that the abatrial ends of the muscles are not carried towards the abatrial side passively, and solely by the growth of the body wall, but that the ends move relatively to the cells of the body wall. A somewhat late stage in the development of the pyramidalis is shown in Figure 63 (Plate VI.). Nearly the whole of the mesoderm of the body wall has here been transformed into muscle cells. The insertion of the muscles is in the mesoderm of the neck of the polypide. (Plate VI. Fig. 63; Plate V. Fig. 45.)

c. Parietal muscles first make their appearance at about the stage of the terminal individual of Plate II. Figure 14, immediately below the bud and to the right and left, i. e. so that the muscles, which usually arise paired, have their long axes parallel to the sagittal plane and perpendicular to the long axis of the branch. They arise from cells of the mesoderm, most of which in this region are filled with vacuoles, and often project into the cœlom. But in my opinion the muscle cells do not themselves arise from such vacuolated cells, for at even an earlier stage (corresponding to Figure 21, Plate III.) one can distinguish thickened patches of elongated cells in the mesoderm which are undoubtedly the young muscle cells; but they do not show the slightest traces of being vacuolated, and in fact are sharply distinguished from the adjacent cells by their uniformly granular appearance and their deeper coloration.

Braem ('90, pp. 124, 125) has already stated that the parietal muscles arise in pairs, and come to traverse the cœlom, not remaining in the body wall. The truth of this statement I can confirm in the case of the parietal muscles first formed, which lie near the future septum. Plate V. Fig. 42 shows the origin of the muscle fibres on both sides of the branch. They have already migrated into the cœlom. As Braem plainly states, the component parts of this pair of muscles, developed from the mesoderm, migrate towards each other and finally fuse into one unpaired mass, as we see in Plate III. Figure 26. It is perfectly evident, in this case at least, that both ends of two muscles originating far apart migrate in some manner towards each other so that the corresponding ends come to lie close together. Such a migration cannot be accounted for merely by growth of the body wall. The ends of the muscle fibres must move relatively to the body wall.

When the muscles have reached their permanent positions in a diameter of the branch, we find their ends attached to the cuticula. As the muscle fibres stain deeply in hæmatoxylin, they can be distinctly traced through the vacuolated and poorly stained cells of the body wall (Plate III. Fig. 26). Figure 29 shows a bit of the wall mechanically separated from the cuticula, the end of the muscle fibre remaining in place. Fine lines can be distinguished in the contractile, deeply staining portion of the fibre. The surface by which attachment is effected appears very slightly crenulated on longitudinal sections of the muscle fibre. I could not distinguish any structural peculiarity on the part of the cuticula to which the muscle was attached, — nothing to indicate how attachment is effected.

Freese ('88, pp. 15, 22, Fig. 11) has described a similar method of attachment of the muscles to the cuticula for Membranipora.[1]

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[1] My friend, Dr. G. H. Parker, tells me that a similar method of attachment of muscle fibres to the cuticula occurs in *Crustacea*. According to Tullberg ('82, pp. 27, 44, 45), the adductor muscle fibres are in Mollusks attached to the cells of the ectoderm. The same condition as in Mollusks seems to exist in Annelids (Eisig, '87, pp. 25, 36).

At a later stage smaller bundles of muscles arise successively toward the neck. These muscles are free from the body wall at their middle region. They do not usually pass through the cœlom in a diameter of the branch, however, but rarely subtend as chords an arc of more than 120°. As Braem supposed, such muscles, although arising later than the most proximal pair, originate in a similar manner to them (Plate VI. Fig. 55). The mesoderm is very thin at the region at which they are first seen, and they are quickly discerned by their larger nuclei and prominent cell body. At a later stage they have grown much longer, and become freed from the body wall at their middle part.

As is well known, there are two *funiculi* in Paludicella, called by Allman respectively anterior (nearer the atrial opening) and posterior. The origin of the funiculi of Paludicella was observed by Dumortier et van Beneden as long ago as 1850. They say (p. 54), "La couche muqueuse une fois formée s'étend rapidement dans l'intérieur et touche bientôt par son extrémité inférieure les parois opposées de la loge. Les cellules muqueuses dont le tout est encore composé contractent de l'adhérence dans cet endroit, et c'est ce qui donne naissance au muscle rétracteur de l'estomac [= funiculi]." Allman ('56, p. 36, Plate XI. Figs. 7–9) also describes and figures very clearly and correctly this process, and Braem ('90, p. 127) has recently confirmed their observations.

It is perhaps unnecessary to redescribe the more evident part of this process, the contact of the polypide with the abatrial wall of the branch. The mesoderm of the bud comes into contact with that of the body wall, the cells of each of the two layers become attached to the other, and by the withdrawal of the polypide the attachment persists at two points forming a long drawn out string of tissue. Figures 36^{a} and 38 (Plate IV.) are contributions to a knowledge of the finer details of this process. Apparently the upper funiculus is developed earlier than the lower, as I have always found it longer at about this stage. The lower funiculus at present consists of only the two mesodermal layers of body wall and polypide intimately united. The funiculus itself consists of a cord several cells thick; but I believe these certainly to be derived from the mesoderm only. Very early some of these cells show an appearance of highly refractive and deeply staining fibres, which I interpret as muscular differentiation (Plate IV. Fig. 38, *fun. su.*), so that the funiculi must be regarded as partly muscular in function. As in Phylactolæmata, these fibres lie near the axis of the funiculus. Braem ('90, pp. 66, 67,) has demonstrated that the muscular fibres of the funiculus of Plumatella pass directly into the muscularis of the body wall. It is interesting to find them persisting in the funiculus of Paludicella, beneath the mesodermal covering, although there is apparently no muscularis developed in the body wall of this region.

8. The Formation of the Neck and Atrial Opening.

This is the last act in the history of the polypide that I shall consider. The body wall around the neck of the polypide continues to possess a less differentiated character than the remaining portion for some time after the oral tentacles have undergone their revolution. One still sees the cells of this region dividing, and the body wall is gradually protruded at this point above the general level. (Plate II. Fig. 14, *cev. pyd.*) The neck of the polypide to which the kamptoderm is attached consists, at a somewhat earlier stage than that just referred to, of a disk of greatly elongated columnar cells in the centre of which there is a distinct notch caused by the presence of shorter cells at that point. (Plate VI. Fig. 63 *b.*) At the inner ends of the columnar cells of the neck lies a flat epithelium quite sharply marked off from the latter, but which is nevertheless undoubtedly derived from the same source as the columnar cells and the inner layer of the bud. This flat layer is directly continuous with the inner layer of the kamptoderm. At a later stage, the columnar cells of the ectoderm become elongated still more, and lose their staining capabilities at their outer ends. Still later one sees them arranged in the form of a cup whose cavity is separated from the outside world only by a cuticula which becomes slightly invaginated at this point. The cells are soon found with their long axes perpendicular to the edge of the cavity they line.

There is one point that I have not been able to determine; namely, how the new cuticula, which is certainly formed at the ends of the cells which lie next to the cavity, becomes continuous with the old cuticula of the non-invaginated body wall, as it is in Figure 50 (Plate V.). The presence on the new unstainable cuticula of the remains of the stainable one, whose origin I have already discussed at length, may serve as a guide to the limits of the old cuticula. The new cuticula is being secreted by cells lying deep in the inner end of the neck, and apparently in one rod-like mass. Unfortunately, I lack stages between this figure and Figure 45 (Plate V.), which shows the neck of a nearly or quite adult polypide cut lengthwise. The solid cuticular rod has now become a hollow cylinder, whose inner (deep) edge is embedded in the deep-lying cells of the neck. Moreover, one finds superficial to the cuticula of the general body wall a second cuticular cylinder, which is free at its outer end, but at its inner end fuses with the surrounding cylinder of cuticula. This inner cylinder, which is probably formed, as Kraepelin ('87, p. 40) suggested, by splitting of the delicate cuticula at the base of the marginal thickening (Randwulst), has been compared by Kraepelin to the "collare setosum" of Ctenostomes. The *Randwulst* itself I believe to be the equivalent of the Diaphragma of Nitsche, as I shall try to show later.

At the deep end of the neck (Fig. 45), the inner layer of the bud is seen to be continuous with the ectoderm. The region of transition may be called the atrial opening, *of. atr.* Surrounding the atrial opening is a fold in the ectoderm, and between the layers of this fold is a thin, non-stainable homogeneous layer, slightly more refractive than the surrounding protoplasm. This membrane extends also a short way into the kamptoderm, and here lies between its two cell layers. Embedded in this homogeneous membrane in the fold, one can distinguish still more highly refractive bodies, *spht.* On account of their form and high refractivity, I believe these to be muscle fibres cut across. The homogeneous membrane has also the same general appearance and relation to the muscularis as the so-called supporting membrane of Nitsche, and it is the only representative of that structure that I have found in Paludicella.

9. Development of the Communication Plate.

In their description of Paludicella, Dumortier et van Beneden ('50, p. 40) say: "Il se compose de plusieurs loges ou cellules placées bout à bout . . . en sorte qu'il n'y a aucune communication entre les différents animaux." Also Allman ('56, pp. 114, 115) refers to the presence of a perfectly formed septum separating the cavities of adjacent "cells." To Kraepelin ('87, p. 38) belongs the credit of having first carefully studied this structure in the adult by means of sections. He came to the conclusion from the appearances which he figures (cf. my Plate V. Fig. 49), that there are small canals passing through the nearly homogeneous central mass, and therefore "dass wir in dem ganzen Apparat eine Vorrichtung zu erblicken haben, durch welche Nährstofflösungen des einen Tieres mittels siebartig wirkender Cautelen in die Körperhöhle des Nachbarindividuums übergeführt werden."

The descriptions of Kraepelin concerning the structure of the "Rosettenplate" are confirmed by my own observations, and seem to justify his conclusions concerning its function. The development of the organ has not, however, been carefully observed heretofore. Korotneff ('74, Plate XII. Figs. 1 and 2) gives figures to show this process, but I have never seen any such circular groove surrounding the branch as he figures. In all cases the two layers of the body wall form a circular fold, in which, however, there is never, even at the earliest stages, a space between the ectodermal layers, nor any infolding of the cuticula as Korotneff ('75, p. 369), according to Hoyer's rather incomplete abstract, maintains (Plate V. Fig. 47). When the circular fold has advanced until only a small pore remains, by which the cavities of the older and younger individuals are kept in communication, the mesodermal cells at the angle of the fold begin to undergo a metamorphosis both in form and histological character. In the first place they become much elongated and extremely attenuated, passing from one surface of the septum to the other, and forming the lips of the pore. In the second place their plasma becomes first deeply stainable, and later, in addition, homogeneous and highly refractive. These metamorphosed cells form what may be called the *teeth* of the plate. They are derived wholly from mesoderm.

The cells in the upper mesodermal layer next increase rapidly in number and size, and the number of teeth is also augmented (Plate V. Fig. 48). The metamorphosis of the cells extends still farther away from the communication pore, and involves the lower mesodermal layer; but, apparently, each cell of the latter is metamorphosed only to a slight depth within its cell wall (Fig. 51), whereas in each of the upper cells the ends which project into the communication pore are modified through and through (Fig. 46). At a later stage (Fig. 49) the metamorphosed part of the cell seems quite sharply cut off from the active part, and the slits between the metamorphosed teeth are considerably reduced. Nevertheless, I believe a transfer of fluids may still occur between them, for even in the adult communication plate one can trace continuous lumina when the cells are by accident torn off from the "teeth" which they have produced. It is important to note that the nuclei are not destroyed in the cell metamorphosis. Some lie above, others below the pore, and become deeply stainable. The ectodermal layers of the communication plate secrete a cuticula between them. This is thinner than that of the body wall, and does not extend, of course, to the centre of the communication plate, but ends in a thickened ring, whose diameter is about one tenth the diameter of the plate, or, absolutely, about 9.4 μ.[1]

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[1] Reichert ('70, p. 267) first carefully described the Rosettenplate of Ctenostomes in Zoöbotryon, and the organ in Paludicella must be regarded as homologous with it. The central circular hole in the cuticula of Zoöbotryon is from 7 to 10 μ in diameter, and from one ninth to one seventh that of the entire plate. Similar

10. RÔLE OF THE MESODERMAL VACUOLATED CELLS.

Allman ('56, p. 36) observed that at the time a lateral branch was well formed, and before the origin of the polypide, the internal outline of the body wall was uneven, and he figures (Plate XI. Fig. 4) very large cells lying on the inside of the body wall. Korotneff ('74, Taf. XII. Figs. 1–3, '75, pp. 369, 370) progressed a step farther, and recognized a distinction between large, coarsely granular cells projecting into the cavity of the bud, especially near the tip, and the surrounding epithelial cells. Braem ('90, p. 126), finally, has described them more accurately. He finds cells filled with numerous granules in the youngest branches of the colony. Immediately around the bud, such cells are less abundant; probably, he says, because their granules have been absorbed in the process of formation of the polypide. He compares the granules with the yolk spherules of the statoblast cells, and believes that they are to be regarded as food matter.

My observations and conclusions, achieved independently of Braem's, fully confirm his. I have succeeded, moreover, in obtaining some additional evidence as to the function of these cells, a subject to which I have paid some attention.

First as to the *distribution* of the cells, and their frequency in different regions. We can best get an approximate idea of this by counting the number of the reticulated cells in each section of a series which involves a young polypide and the regions immediately above and below it. It is not possible to do this with perfect accuracy, because there is no sharp line of distinction between reticulated and non-reticulated cells; but I have made the count without prejudice, and I believe as fairly as possible. When the bud of the polypide has reached about the stage shown in Plate III. Figure 28, the number of reticulated cells seems to have nearly reached a maximum. In the series from which this figure was taken there was an average of 4.8 reticulated cells to the section in the ten sections distal of the bud. There was an average of 11.2 reticulated cells to the section for the twenty sections which passed through the bud, and 11.2 for the eleven sections proximal of the bud in the region

perforated organs have been described by Smitt ('67, p. 426), Nitsche ('71, pp. 420–422), and Vigelius ('84, p. 26) for Flustra, by Freese ('88, p. 7, 13, 14) for Membranipora, by Ostroumoff ('86ª, p. 13) for Lepralia, by Claperède ('70, p. 160) for Bugula and Scrupocellaria, by Ehlers ('76, p. 14) for Hypophorella, and by Joliet ('77, p. 222) for Bowerbankia. Nitsche alone ('71, p. 455) has had anything to say upon their origin, and this apparently not the result of direct observation.

at which muscle fibres were arising. A similar series through a slightly older bud gives for the same regions respectively 5, 14, and 13 cells per section. In series through older buds, a rapid decline in the number of these cells occurs so that at the stage of Figure 30 (Plate IV.) there is an average of only about 3.1 cells per section through the bud, and about 2.2 immediately below. These reticulated cells are not very numerous in the region of the bud at the time this is about to arise, as a look at the sections Figures 3 and 4 shows. One finds reticulated cells in the mesoderm at the tip, and most abundantly at a rather early stage in the development of the bud. The number of these cells diminishes as one leaves the young individual to pass into the next older of the same branch. In the adult such cells are rather rare; so rare, in fact, that Kraepelin ('87), who studied with care the body wall of the adult individual, makes no mention of them. Nevertheless they do occur in the cells which are to go into the lateral branch (Plate II. Fig. 15), as well as elsewhere on the body wall. The place in which one finds the reticulated cells most abundant, however, is in the young *lateral* branches near the time when the polypide bud is about to arise. Here every cell of the mesoderm is greatly enlarged, and filled with the vacuoles (Plate VI. Fig. 58). These are very apparent upon a surface view of the branches. Reticulated cells occur not only in the mesodermic cells of the body wall, but also in those of the polypide bud, which were, indeed, only lately a part of the mural mesoderm (Plate III. Fig. 28, Plate VI. Fig. 56). Thus, in general terms, we may say that the reticulated cells of the mesoderm are chiefly confined to regions in which there are young buds developing; and since these arise at intervals only, there is a periodicity in their appearance, — a time of maximum development followed by one of decline, then one of reproduction of such cells in the ends of branches culminating in another maximum, and so on.

Turning our attention now more particularly to the *structure* of these reticulated cells at the period of their best development, we find (Plate VI. Figs. 56, 57, 59) that they possess a large nucleus lying at the deep end of the cell and containing a relatively large nucleolus, and that this is surrounded by a granular protoplasm with included vacuoles. It is very common to find the nuclei in various stages of division, and thus it is frequently seen as a mass of chromatic substance without any nuclear membrane or nucleochylema. The vacuoles, which in the more regular cells lie in a semicircle nearly peripheral (the nucleus being at the centre), are highly variable in number, some of the cells containing as many as 20 to 30. They often appear as perfectly clear homogeneous spaces, but more frequently at this stage contain a spherical body, which frequently fills the entire vacuole and is more refractive than the surrounding plasma (Fig. 59). Not unfrequently one sees a less refractive, clear space, surrounding the highly refractive body (Fig. 57).

The description just given corresponds to the condition seen in a terminal branch whose polypide has attained the development of that shown in Figure 28 (Plate III.). At the time immediately preceding the origin of the bud, the cuboidal cells of the mesoderm show traces of vacuolation, but their form and size have suffered no appreciable disturbance. This vacuolation of cells proceeds hand in hand with the development of the bud, and one first notices the homogeneous, highly refractive bodies in the vacuoles when the bud is well established. At about the time the alimentary tract has become formed, the reticulated cells begin to show signs of degeneration. The highly refractive bodies have disappeared, and the skeleton of the cell which remains becomes very irregular. As already stated, the number of reticulated cells also decreases, until, at about the time of "rotation" of the polypide, there are few reticulated cells in the mesoderm, but these few are filled with vacuoles and their highly refractive bodies.

The conditions of the mesodermal cells at the tip are slightly different from those found elsewhere. Usually, instead of many small vacuoles, one finds only one or two which fill almost the entire cell, — sometimes perfectly homogeneous in structure, sometimes containing small highly refractive granules.

These appearances I believe to be explicable only upon the assumption that *the mesodermal cells are capable, at the time at which the young polypide is arising, of imbibing the fluids of the body cavity and storing them up for the purpose of supplying the rapidly growing cells of the bud with nutrition.* It is desirable to show reasons for believing, first, that the contents of these cells are nutritive matter; secondly, that this has been taken up from the body cavity; and, thirdly, that it is supplied to the bud for its nutrition.

It must be admitted that the strongest argument for the belief that these are absorbing cells is derived from a comparison of the appearances which we find in these cells with those described for Protozoa, and by Metschnikoff ('83, Taf. I. Figs. 18–35) for mesodermal trophic cells. At the same time, it must be acknowledged that similar cells are found in other cases where the function is believed to be not ingestive, but excretory, as in the chlorogogen cells of Annelids, as shown by Kükenthal ('85), Eisig ('87, pp. 751–762), and others, and indeed even in the cells of cœlomic epithelium. Eisig ('87, p. 752) has already clearly expressed how, in view of the many cases of high excretory activity of peritoneal and blood cells demonstrated by him, "künftighin bei der Beurtheilung gewisser Zelleneinschlüsse erst genau festzustellen sein wird, ob man est mit *von aussen aufgenommenen* (gefressenen), oder aber mit von der Zelle *ausgeschiedenen* Producten zu thun habe."

A criterion for judging this matter may be found, in the first place, I believe, in this: that the products of excretion increase with the activities of the cells, and are thrown out, usually in the shape of concrements, either *from* the cell or *with* the cell into the cœlom; whereas bodies taken in from without for digestion decrease with the activities of the region. In the second place, vacuoles are less characteristic of excretory tissue than of imbibitory. But vacuoles are the important feature of the reticulated cells in Paludicella, and the highly refractive bodies are less constant phenomena. As for the latter, they are not found in the later stages, nor in the earliest. Moreover, these bodies differ from excretion concrements in this, that they are always transparent, often almost indiscernible in the vacuole, except by their higher refractiveness, and there is no sharp demarcation between cases of vacuoles filled by such bodies and those the contents of which are less highly refractive. The degree of refractiveness is variable, at one end of the series grading off into the undifferentiated fluid of the vacuole. What significance is to be assigned to these highly refractive bodies in the vacuoles? There are two reasons why I do not believe that they represent solid food particles devoured as such by the mesodermal cells. First, I do not find such highly refractive bodies lying loose in the body cavity before the stage at which they first appear in the cells; and, secondly, one can find all gradations between less highly refractive vacuoles and highly refractive ones (which I have assumed to be entirely filled by one highly refractive body), and between the latter and vacuoles containing a small body surrounded by a broad, clear area. I believe, therefore, that the vacuoles are rather cavities filled with chemically different nutritive fluids, which are acted upon differently by the reagent.

I have assumed that the contents of the vacuoles represent material taken up from the body cavity, because it seemed most reasonable to look there for the source of their supply. The ectoderm is covered on its outer surface by an apparently continuous cuticula, so that food cannot be gained from the outside world directly. It is, moreover, not unreasonable to suppose that some of the products of digestion elaborated by the adult polypides of the colony pass through the wall of the partial penetration of the mesoderm on each side into the space between these two layers (Plate IV. Fig. 30, *ms'drm.*). At a later stage the mesoderm may be seen as a single cell layer lying between the ectoderm and the inner layer of the bud midway between the oral and anal ends (Plate IV. Fig. 32, *ms'drm.*), and as a double cell layer at the oral end of the bud (Fig. 34, *ms'drm.*). It is from these cells at the oral end of the bud that the retractor muscles are to arise (Plate III. Figs. 23–25, *cl. mu. ret.*). As the oral end of the kamptoderm and œsophagus to which their inner ends are attached moves away from the ectoderm, and as the area of the latter itself increases, the two ends of the cells move farther and farther apart, and the young muscle cells become drawn out into spindle-shaped muscle fibres. (Plate III. Fig. 25, *cl. mu. ret.*; Plate IV. Fig. 36, *mu. ret.*) The retractor thus arises unpaired and remains so at its origin, but nearer its insertion in the ring canal and œsophagus one can distinguish a division into right and left masses. The adult muscle fibres consist of two parts at least, the inner contractile portion and an outer less modified protoplasmic portion, which can be traced over the whole of the first part, but is most evident around the nucleus, where it has a granular appearance.

b. Pyramidalis. — At about the stage of Figure 25 (Plate III.) one finds, on cross sections of the branch which pass through the neck of the polypide, that the mesoderm of the body wall on each side of the neck is greatly thickened, and that its closely packed cells, which lie three or four deep, have become somewhat elongated. Cell division is quite common in the ectoderm of this region, and by it the area of the circumcervical region is increased and the two ends of the muscle fibres are carried farther apart, one end remaining attached to the neck of the polypide and the other moving towards the abatrial surface. I have given reasons above (page 16) for believing that the abatrial ends of the muscles are not carried towards the abatrial side passively, and solely by the growth of the body wall, but that the ends move relatively to the cells of the body wall. A somewhat late stage in the development of the pyramidalis is shown in Figure 63 (Plate VI.). Nearly the whole of the mesoderm of the body wall has here been transformed into muscle cells. The insertion of the muscles is in the mesoderm of the neck of the polypide. (Plate VI. Fig. 63; Plate V. Fig. 45.)

c. Parietal muscles first make their appearance at about the stage of the terminal individual of Plate II. Figure 14, immediately below the bud and to the right and left, i. e. so that the muscles, which usually arise paired, have their long axes parallel to the sagittal plane

That the nutritive matter in the cœlomic cells is supplied to the young bud is what we should expect, since the cells of the bud, being most actively engaged in growth, will require most nutriment. The actively dividing cells of the outer layer of the bud are thick and cuboid, and are rarely so highly vacuolated as the more passive ones of the body wall; yet occasionally one finds one or two huge cells in this layer full of vacuoles, which contain highly refractive bodies. In most cases these cells send out processes into the cœlom, and in a few instances I have seen them united with similar processes from cells on distant parts of the body wall. This remarkable phenomenon, shown in Figure 54 (Plate VI.), may possibly signify that cells of the cœlomic epithelium at times directly communicate with those of the outer layer of the bud to supply it with nourishment. Nutrition of the bud is also probably effected through the presence of large reticulated cells at the angle between the bud and the body wall. A condition like that shown in Figure 56, *cl. ret.*, is very common.

Every author from Dumortier et van Beneden to Braem, who has studied the origin of the polypide in Paludicella, has mentioned the presence of highly refractive bodies in the alimentary tract at the time of its formation. These are very striking in *some* living specimens, and in whole animals after killing. I have found that this highly refractive substance in the bud is exceedingly variable in amount and position, and that sometimes it is apparently absent. When present, it usually occupies the lumen of the forming alimentary canal; but, as sections show, it is often located in large vacuoles in the future digestive cells of the alimentary tract. It seems highly probable that, as Braem suggests, this is nutritive substance, and it has doubtless come from the body cavity through the agency not only of the outer layer of the bud, but also of other parts of the cœlomic epithelium.

I am inclined to interpret the phenomenon of cells filled with nutritive material as an adaptation to the peculiar conditions of Paludicella, in which the individuals are early separated from one another, except for the communication plate, through which at best fluids can pass only slowly, and in which a rapid growth of the body wall to produce the polypide takes place periodically. The mesodermal cells rapidly absorb the nutritive fluids of the body cavity and store them in their substance before the formation of the communication plate, and give them out again during the period of the polypide's most rapid growth chiefly to this part of the individual. This hypothesis has been mainly derived from considering the fact of the great development of the reticulated cells in the lateral bud and the very early completion of its communication plate, the immediate needs of the polypide, which arises only after the formation of the plate, being met by this supply of stored nutriment.[1]

But why is the septum (communication plate) formed so early, if it is desirable for the species that the growing tip should be well nourished by the fluids of the body cavity? Here again I must resort to pure hypothesis. I assume that the early formation of the septum is a provision for the protection of the stock against a rapid influx of the surrounding water in case the branch is broken. One can understand how, if the body wall and growing regions depend upon the fluids of the body cavity for nutrition, an open communication of this cavity with the outside world would be a serious obstacle to regeneration of the body wall in the lost part, or the growth of the stock in any other direction. There is a fact which ought to be mentioned in this connection, as bearing on this hypothesis of the function of the septæ. One frequently finds that in stocks which have been handled with reasonable care the median branches are broken off at either end, and in almost every colony one or more lateral branches are missing from the parent branch. Apparently, then, the lateral branches are unusually subject to destruction, and we find the septæ developed at a much earlier period between them and the ancestral branch than between individuals of the median branch. Compare Plate II. Figure 14, in which the communication plate has not yet begun to form, with Plate VI. Figure 58.

III. Budding in Marine Gymnolæmata.

1. ARCHITECTURE OF THE STOCK.

I have already described the process of stock-building in Paludicella, and have attempted to show that it follows a certain law. I desire now to present a few observations upon the architecture of certain stocks of marine Gymnolæmata, which will aid in arriving at some general conclusions later on. Other observers have worked out the architectural laws of single species or groups, and I shall refer to their studies either in connection with the species which I have used in common with them, or in the general part of this paper, in considering the process of budding in Bryozoa as a whole.

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[1] Similar conditions to those in Paludicella exist in some marine Bryozoa, and in one of these cases, Bowerbankia, I find them fulfilled by a similar arrangement. The young buds of the stolon which give rise to the "nutritive zoöids" are, at an early stage, loaded with food granules. As in Paludicella, so in Bowerbankia the communication plates are formed early.

I will begin my description with *Bugula turrita*[1] of Verrill, which I gathered in the summer of 1889 at Wood's Holl, where it occurs abundantly on the piles of the wharf. The stock is bushy, and, when its polypides are active, of an orange color. In its simplest form the stock consists of a central axis, which is somewhat zigzag, and gives off lateral branches like the trunk of a tree. The lateral branches are inserted on the trunk in a spiral line. Each lateral branch is fan-shaped (Plate VII. Fig. 64), the part corresponding to the handle of the fan being the point of attachment, and the fans are smaller the nearer they are to the tip of the trunk. The attachment of the branch to the trunk is effected by one primary individual. Each fan-shaped branch extends from its point of attachment obliquely upward and outward, and, although it is slightly concave on its upper inner surface, the concavity is not sufficient to prevent its being spread out upon the slide for study without materially disturbing the interrelation of the individuals in the stock.

I have studied several branches flattened in this way (one of 400 individuals), and have made camera drawings of them. Since the results in the different cases are substantially in agreement, I have concluded that they are significant. One of these camera drawings is shown in the figure just referred to.

To designate individuals in the stock, I have adopted a simple nomenclature. The forty-four terminal individuals are numbered from 1 to 44. The successive generations (if I may be allowed to use this word in a loose way) are indicated by the Roman numerals from I. to XIII. Any one individual is indicated by placing the numbers of the radial line or lines to which it belongs first, and following this by the Roman numeral of the generation to which it belongs. Thus, 27–30 IV. is an individual near the base of the twig 27–30 and of generation IV. Figure 64^a (Plate VII.) is a diagram showing the arrangement of the individuals in Figure 64. The radial lines represent the rows of individuals; the concentric lines separate adjacent individuals of the same radial row. The same nomenclature is used as in Figure 64.

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[1] This species is very similar in general habit to B. avicularia, Linnæus, and to B. turbinata, Alder (Hincks, '80, pp. 75–80). It differs from the first named species by possessing only one spine, on the outer upper edge, as described by Leidy ('55, p. 142), instead of having three, — two outer upper and one inner and upper. It differs from Hincks's diagnosis of the second in having only two "cells" in each branch, instead of 3–6 in the upper portions. The form of the avicularium would seem to ally it more closely to B. avicularia.

In studying Figures 64 and 64^a, one of the first facts which attracts our attention is that (1) *the individuals of the twigs are in pairs, and the adjacent individuals of the two rows "break joints."* In general, one finds that the individuals of the same twig are of the same length; but since the two rows of any twig ultimately rest upon one, either the proximal two individuals of these rows must be of unequal length, or else they must arise on different parts of the individual which supports them. Both of these cases occur. Sometimes one individual (26 IX.) has nearly twice the length of the other (25 IX.), and in other cases (9, 10 VI., 11, 12 VI.) the more proximal of the two individuals (9, 10 VI.) arises so far proximally on the side of the supporting individual 9–12 V. as to have a total length quite equal to that of the more distal (11, 12 VI.). Owing to their different positions upon the individual 9–12 V., these two individuals may be designated as lateral (9, 10 VI.) and terminal (11, 22, VI.). *The terminal individuals continue the ancestral row; the lateral individuals are the first of lateral branches.*

This distinction is an actual, and by no means a meaningless one. The constant difference in position of the two individuals which rest upon one shows conclusively that this branching cannot be regarded as dichotomous, and I may say parenthetically that I shall try to show in the general part of this paper that true dichotomy is not common in Bryozoan stocks, if indeed it exist at all. Now, since in the rows of individuals in which there is no lateral budding the distal lies directly terminal to the proximal individual, that individual which fulfils this condition at the region of bifurcation of the twig must be regarded as continuing the ancestral branch; and that individual, conversely, which arises from the side of the single proximal individual must be regarded as the lateral one. Thus we have the stock composed of ancestral and lateral branches as represented in Figure 64^a.

(2) *When two lateral branches are given off from two ancestral ones which have had a common origin* (and are consequently themselves respectively ancestral and lateral branches), *they are given off towards each other.* This is equally true whether the two lateral branches in question arise in the same generation (32 X., 33 X.) or in different

generations (24 X., 25 IX.). This may be expressed by saying branches are given off on the side towards the axils.

By consulting Figure 64ᵃ and tracing out the finely dotted lines which connect the second, third, etc. axils of all branches counting from the proximal end of the fan, it will be seen that (3) *lateral buds tend to arise on two closely related branches in the same generation.* There are several slight deviations from this rule. The less closely related the branches, the less marked the tendency, although it is still discernible. (Cf. branches 9–16, 23–30.)

This rule does not hold, however, so well on the margins as in the middle region of the fan, for here another and a superior rule seems to obtain. This is that (4) *lateral budding occurs more frequently at the margins of "fans" than elsewhere.* Thus in Figure 64ᵃ there is at the margins, on the average, 1 case of lateral budding to 4.3 cases of median budding. Elsewhere the average is as 1 to 6.5. In larger fans the difference is even more pronounced. This is true not only for the "fans," but also, to a less degree, for the two "subfans" which arise respectively from the two individuals of generation II. (but 17, 18 is very anomalous in this respect). In general, any rule deduced for the margin of the fans holds true also for subfans to any degree of subdivision; but the less perfectly, the higher the degree.

By consulting again the diagram, it will be seen that the branches have attained different lengths. Thus 9, 10, 29, and 30 contain representatives of generation XIII., while the terminal individual of branch 1 is of generation X., and those of branches 35–44 are of generation XI. So the curve which connects the tips of the branches (see dot-and-dash line, Fig. 64ᵃ) would rise from 1 to 9–10 as a maximum, and fall again till it reached the margin of the first subfan; then rise again, reaching a second maximum in the middle at 29–30, and finally fall again to the other margin. In general, then, (5) *the marginal branches are shortest, the intermediate ones longest,* i. e. *give rise to the greatest number of generations.*

Although the marginal individuals of say generation III., IV., or V. do not support branches with so many generations as the intermediate ones, yet they are not therefore necessarily less prolific in individuals, because the number of branches arising distally of such individuals is greater according to rule 4 than the number arising distally of the intermediate ones. Thus, if we count the number of individuals borne on each of the eight individuals of the fourth (IV.) generation of Figure 64, we find in the given case: —

Outer.	1.	1–8 IV. (an outer individ.)	gives rise to	8	branches	and	34	individ.
	2.	9–12 IV. (an inner ")	" "	4	"	"	27	"
Inner.	3.	13–16 IV. (an inner ")	" "	4	"	"	23	"
	4.	17, 18 IV. (a subouter ")	" "	2	"	"	13	"
Inner.	5.	19–22 IV. (a subouter ")	" "	4	"	"	25	"
	6.	23–26 IV. (an inner ")	" "	4	"	"	23	"
Outer.	7.	27–30 IV. (an inner ")	" "	4	"	"	26	"
	8.	31–44 IV. (an outer ")	" "	14	"	"	56	"

According to the rule that inner branches are slightly prolific, we should expect cases numbered 4 and 5 in the above table to contain the fewest branches and individuals; in accordance with the rule that marginal branches even of subfans are more prolific, we should expect them, on the contrary, to contain more branches and individuals than cases numbered 3, 6, etc. The result is usually a condition intermediate between that of the middle and outer branches, such as is partially realized in case number 5. Case number 4 seems to present an unusual condition, which may be correlated with the fact of its close approximation to number 5. (See Fig. 64, 17–20.) From the consideration of this and other cases, I think this conclusion may fairly be drawn: (6) *Of the four proximal individuals from which a fan arises, the outer two will bear the greater number of individuals, the inner two the lesser.*

Since from rule 2 median individuals (ancestral branches) occupy the margins of fans (or subfans of any degree) and the lateral branches are intermediate, it follows, as a corollary to rule 5, that, in general, the ancestral branches are the shorter, the lateral branches the longer; and, as a corollary to rule 6, that from any axil the ancestral branch will of the two give rise to the greater number of individuals; the lateral branch, conversely, to the less, other conditions being equal.

We have deduced the laws of lateral budding on different parts of the circumference. We find also that there is a regular variation in the frequency of lateral budding, dependent upon the distance of the region from the primary individual of the fan. This rule, like any other, is not invariable, whatever the other conditions may be; but it is more or less dependent upon them. A small and regular fan having seven generations gives this result.

No. of Generation.	Number of Individ.	Increase per Cent.
I.	1	
II.	2	100
III.	4	100
IV.	8	100
V.	12	50
VI.	16	33⅓
VII.	16	0

In this table the first column gives the number of the generation, the second the whole number of individuals in the generation, and the third column the increase per cent of individuals in each succeeding generation over the last. In this specimen the increase underwent a very regular diminution.

With larger colonies so great a regularity as that just shown is hardly to be expected, nor is it found. The following table is based on Figure 64, and is like the preceding; but in addition the percentage increases have been averaged — i. e. the means of successive increases taken in pairs have been given — to eliminate what may be called accidental variations.

Generation.	Number of Individ.	Increase per Cent.	Average.	Generation.	Number of Individ.	Increase per Cent.	Average.
I.	1						29
				VIII.	28	27	
II.	2	100					23
			100	IX.	33	18	
III.	4	100					18
			100	X.	39	18	
IV.	8	100					16
			88	XI.	44	13	
V.	14	75					
			49	XII.	20		
VI.	17	22				Incomp	lete.
			26	XIII.	4		
VII.	22	30					

Hence we conclude, *There is a diminution in the rate of increase of individuals in the "fan" as it grows older.*

In searching for an explanation of this phenomenon, I first drew a line from the centre of the primary individual of the fan to the periphery, and divided it into four equal parts. I then described arcs with the primary individual as a centre, and with radii equal to $\frac{1}{4}$, $\frac{2}{4}$, $\frac{3}{4}$, and $\frac{4}{4}$ of this line respectively. Counting the number of individuals cut by these arcs respectively, and dividing those numbers by the length of the corresponding arcs, I found that *there is almost exactly the same number of individuals per unit of arc for each of the four arcs.* (Rule 7.) The previous conclusion, that there is a diminution in the rate of increase of individuals in the fan as it grows older, may then be considered as a corollary to this rule, as it obviously follows from it.

Bugula flabellata, J. V. Thompson.[1] — I have studied this species for the purpose of confirming the results obtained in B. turrita, and have found the architecture of the two species alike in all essentials.

The entire colony of B. flabellata (Plate VII. Fig. 66) may be compared to a single "fan" of B. turrita, only there are usually many more individuals in the former, and of course there is no central stem to which it is attached; but the fan is fastened directly by its rhizoids to the object which supports it.

Usually about four rows of individuals are united, instead of two as in B. turrita, — a condition which can be easily derived from the latter by imagining adjacent branches to become fused together. Here as there adjacent individuals break joints. Here as there lateral branches are given off towards the axils.

Rule 3 is not true for B. flabellata. This is entirely annulled by the establishment of a new rule, which depends upon the new conditions found in this species; namely, that more than two rows cling together, and that consequently one or more rows of individuals are enclosed between outer marginal rows. In any such twig composed of more than two rows (Rule 3a) *lateral branches are given off only from the marginal rows.* (See Fig. 66, 49–54 XVII.) It might possibly result, then, that certain of the middle rows of the twig should never give rise to lateral branches. But I do not believe that this ever occurs in very long rows, for by the splitting up of the twigs the middle rows sooner or later become marginal (so 46–51 XV.). In one stock that I have drawn, consisting of 17 to 21 generations, every middle row occurring as such up to the 13th generation had become at the periphery a marginal row.

As in B. turrita, so in B. flabellata lateral budding occurs most frequently at the margins of fans, — in a fan of about 800 individuals in the ratio of 1 : 10 for the margin, and 1 : 14 for the remainder of the fan. By a comparison of these figures with those given on page 43 for B. turrita, it will also appear that lateral budding is less frequent here relatively to terminal budding than in B. turrita.

The fifth rule deduced for B. turrita holds equally well here. In one case the curve of the tips of the rows rises from the margin of the fan at generation XXIV., reaches 3 maxima of XXVI., XXVII., and XXVIII. respectively, and falls again at the other margin to generation XXIII. In the subfan from which Figure 66 was taken, the curve begins at the outer margin with generation XVII., rises to generation XXII. at two points, and falls again to XX. at the inner margin of the subfan.

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[1] The species which I have studied is identified by Verrill ('73, pp. 711, 389) under this name, and my specimens also agree fairly with Hincks's ('80, pp. 80–82) diagnosis. The two pairs of spines, one longer than the other, could be distinctly seen. Hincks says, "The rows of cells . . . are never, I believe, fewer than four, and range as high as seven." But his Figure 66 shows three rows only in some places.

Of the four proximal individuals in any fan here, as in Bugula turrita, the outermost, ancestral give rise to the greater number of individuals. In one case, for instance, the marginal individuals lie at the base of 31 rows with 184 individuals, while the inner ones support only 7 branches with 65 individuals. Similar results were obtained from other stocks.

With the middle of the primary individual as a centre, I passed an arc of a circle through the extremities of the branches of a large camera drawing of a fan of B. flabellata, divided the radius into eighths, and passed arcs through these points. The number of individuals cut by the different arcs was then counted and tabulated; the arc with the longest radius cut through 87 individuals. By measuring the length of the arcs, the number which should be cut by each arc on the assumption that the number of individuals per unit of arc is constant for all radii was determined. This was then compared with the actual number found, with the following results: —

Length of Radius.	No. of Individuals observed.	Theoretic No.	Length of Radius.	No. of Individuals observed.	Theoretic No.
1	3	2½	5	37	40
2	7	6	6	56	56
3	13	13	7	68	70
4	22	25	8	87	[87]

In this instance, then, the 7th rule deduced for B. turrita evidently holds true for B. flabellata.

While at Mr. Agassiz's laboratory at Newport, during the summer of 1890, I had frequent opportunity to examine other stocks of Bryozoa, which occur there very abundantly. I will take four species as typical examples of the groups they represent, and treat of the architecture of their colonies.

Lepralia Pallasiana, Busk.[1] — It is not at all easy to determine from a young stock what has been the order of succession of individuals. One has to view the object from both sides, make a careful examination of the walls of the zoœcia and of the relation of the polypides to one another, and, when he has done his best to determine what are the facts, he must feel that his conclusions are after all more or less subjective. By a careful study of the colony shown in Figure 71, I have constructed the diagram shown in Figure 71^a.

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[1] I do not feel perfectly certain that the specimen shown in Figure 71 (Plate VIII.) belongs to this species, because the characters of the young stocks differ some-

The stock of Lepralia is a creeping one, and all of its rows of individuals are in juxtaposition. This juxtaposition is continued into the adult stage. Even the young stock begins to show evidence of a quincunx arrangement of individuals. This is less evident in the youngest individuals than in the older part of the stock, and is most evident in old colonies. That there is not here a true dichotomous division of rows of individuals, resulting in the annihilation of the ancestral row and the establishment of two new ones, is evident from a glance at the youngest generation in rows 11, 12, or, better, 2, 3, in which the relation of terminal (11, 3) and lateral (12, 2) individuals is very different. The former continue the ancestral line, the latter establish new rows. Lepralia differs from Bugula in this: that two lateral branches may be given off from the ancestral row in the same generation, as at *B*, *C*, and *a*, *a* (enclosed in circles), Figure 71^a.

In contradistinction to the conditions in Bugula, when only one branch arises, it is not given off towards the axil, but away from it.

The synchronism of the budding process noticed in B. turrita is hardly distinguishable in the adult stock of this species; in the young, however, it is quite marked, and gives to the whole a very symmetrical form. The cleavage of eggs does not proceed by more regular steps. Of the three individuals *a*, *C*, *a* (in circles), which follow *B*, each has given rise to three others, a median and two lateral. From each of the three individuals derived from the two individuals *a*, *a* (in circles) has arisen a lateral branch. Rule 3 is therefore well marked in the young stock of Lepralia.

Rule 4, concerning the greater frequency of lateral budding at the margin, is also exemplified in Lepralia. The ratio of cases of lateral to median budding being 1 : 1 on the margin (rows 1–6 and 15–19) and 1 : 2.8 in the middle (rows 7–14.)

In Bugula, as will be recalled, it was concluded that the marginal

what from those of older ones. Yet it is an Escharine closely allied to Lepralia, and I have seen in some cases the broad-based spine on the proximal border referred to by Verrill as being found in L. Pallasiana.

branches were possessed of fewer generations than the intermediate ones. Since by Rule 2 the lateral branches were given off towards the axils, and the ancestral branches therefore always remained marginal, it resulted that the ancestral branches were the shorter, the lateral branches the longer. But in Lepralia lateral branches are turned away from the axils, and here we find the conditions concerning the relative number of generations in marginal and intermediate rows correspondingly reversed. Thus, in Figure 71^{a}, the terminal individual *D* of row 10, a median but ancestral row, belongs to generation IV. while the lateral branches 6 and 15 have five generations of polypides. Thus it is true here, as in Bugula, that the ancestral branches are the shorter, the lateral branches the longer (page 44).

That the outer individuals *a*, *a*, of rows 6 and 15, have given rise to more individuals than the inner *C*, is clear without further comment. Finally, since the individuals retain a nearly constant width, the necessity of the rule established for Bugula, — viz. that there is almost exactly the same number of individuals per unit of arc for all radii, — and of its corollary, — that the increase of individuals in sucessive generations undergoes a regular diminution, — is apparent.

Flustrella hispida, Fabricius.[1] — This stock is a very dense corm-like one. The primary individual becomes surrounded on all sides by the younger zoœcia. It is very evident from an inspection of the position of this primary polypide with relation to the periphery, that growth occurs most rapidly on each side and in front of the primary polypide. In making any diagram of such a stock, it is not very difficult to decide upon the origin of the more peripheral individuals of the stock, but it is wellnigh impossible to say with any certainty what are the relations of the individuals of the second generation to those of the first. Barrois ('77, pp. 227–229) has, however, determined this for this species, and my diagram (Fig. 67) is based in part upon his observations. I do not desire to insist that the diagram represents the exact method of growth of the stock. It is an attempt to represent it, founded principally on careful study of Figure 69. The quincunx arrangement of individuals is already apparent in the young stock (Fig. 69); it becomes more evident in the adult, and when new individuals arise distad to any two, one of the new ones is median (ancestral branch), the other lateral. (So terminal individual of rows 11 and 10; 22, 23; 43, 44; etc.) In the diagram, however, I have not always indicated which is the median and which the lateral branch, for in the older parts of the colony, owing to a shoving of individuals, it is not easy to distinguish them.

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[1] Hincks ('80, pp. 504–506) makes the existence of a larval bivalve shell a characteristic of this genus, and therefore I assign to it a very common Alcyonidium-like form which was extremely abundant on Fucus at Newport. F. hispida is the only species of this genus. I found the bivalve shell still adhering to the primary individual of a young colony (Plate VIII. Fig. 69, *o*.). In Verrill's ('73, p. 708) catalogue this species is referred to under the name "Alcyonidium hispidum, Smitt."

Lateral branches appear usually to be given off towards the axis. Here, as in Bugula, the lateral branches tend to be longer; the ancestral, shorter.

It is evident from the diagram that lateral budding is most frequent at the margins of the corm, i. e. that part lying posterio-dextral or posterio-sinistral of the primary individual, and that the descendants of the two lateral individuals of the four belonging to generation II. are more numerous than those derived from the middle two. Finally, it is evident that the number of individuals per unit of arc will be the same for arcs of all radii, and therefore the rate of increase of individuals will diminish through successive generations.

In *Crisia eburnea*, Linn.,[1] we find the same laws illustrated. The architecture of the genus has been carefully treated of by Smitt ('65^a, pp. 115–142) as forming the basis of classification. Barrois ('77, pp. 76–85) has described in a masterly way the formation of the young stock of tubuliporid Cyclostomata, and the relationships of the different types of budding in this group. Harmer ('91, pp. 145–173) has recently discussed the architecture of the stock in British species, adopting Smitt's graphic method of showing it. I have found his paper of great value for my purpose.

This species grows as a shrub-like stock upon floating eel-grass, etc. I was wrong in saying, in my Preliminary ('91, p. 282), that Crisia has its branches united in pairs. The comparison of this species made by Barrois ('77, p. 82) with the "geniculata form" is conclusive evidence, to my mind, that the apparent double row is in reality a single one, and that such a branch as 18, Figure 65, is to be represented by a single line in the diagram Figure 65^a. We find here terminal and lateral branches; no true dichotomy. Branches are given off on the side *away* from the axils, as in Lepralia, not as in Bugula. (But branch 11 is an exception to the rule.) They are given off, as Harmer ('91, p. 131) has shown, alternately to the right and left.

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[1] This is the only species of Crisia given by Verrill, and, since my species is very common, it must be the one to which he refers. Moreover, it agrees fairly well with Harmer's diagnosis ('91, p. 131).

There is something of a tendency for lateral branches to be given off in the same generation from closely related branches. Thus (Fig. 65^a) from the primary individual, *o*, of the stock, two individuals, a median and a lateral one, arise. Each gives rise in its first generation to two individuals, a median and a lateral. Of these four individuals each gives rise at the end of three generations of median buds to two buds, a median and a lateral. Comparing 2 and 10, first descendants of the two branches arising from the second individual of 8, we find that each gives rise to lateral branches from their first individual and from their fourth. Comparing 14 and 19, first descendants of the two branches arising from the first individual of 8, we find each giving rise to lateral branches from their first individuals. The law breaks down, however, when an attempt is made to carry it to extremes.

The fourth rule is not always so pronounced in Crisia eburnea as elsewhere, although lateral budding seems to be slightly more frequent at the margin.

The extreme marginal branches usually attain far fewer generations than the more intermediate ones; thus, in Figure 65^a, branch 20 ends in the 7th generation and branch 13 in the 7th also, while the more intermediate branches 15 and 18 attain 12 and 14 generations respectively. So, too, while the outer branches 6 and 1 contain respectively 10 and 11 generations, the inner branches reach 12 and 14.

It is very noticeable that the outer branches give rise to more individuals than the intermediate ones. Figure 65^a will serve to illustrate this also. Here the outer branch 4, the intermediate 8, and the outer 15 possess, together with the branches arising from them, 33, 28, and 40 individuals respectively. Harmer ('91, p. 168) finds this true for his Crisia ramosa, for he says, "It is frequently remarked that the longest and most branched parts of the colony are lateral branches, and not parts of the main stems."

There is, in the long run, a decrement in the rate of increase of individuals in successively older generations, yet it is not so regular a one as that which we found to exist in Bugula. Thus, in the seven generations which even the shortest branches shown in Figure 65^a had attained, the average increase of the number of individuals in the second, third, and fourth generations over the number in the preceding is 67%; in the fifth, sixth, and seventh, 44%. The generations beyond the seventh are not complete; they would have contained more individuals at a later period, when the branches which have now attained only seven generations had grown. Thus the number of individuals in successive generations beyond the seventh increases more and more slowly, and finally decreases to zero. Thus the average rate of increase of individuals in the generations 7 to 10 over those in the preceding is only 16%.

One finds here, as elsewhere, that the number of individuals cut by any unit of arc, the primary individual being taken as a centre, remains practically constant, whatever the radius of the arc.

In studying the creeping stocks of Cheilostomes (Plate VIII. Fig. 71), young corms have been chosen because they exhibit fewer irregularities of formation than old ones. Such irregularities are chiefly due to some unevenness of the surface on which the corms lie, but sometimes apparently to a crowding of individuals. Old rows of individuals are occasionally entirely cut off and end in the middle of the stock; sometimes two rows running side by side, perhaps derived from a common ancestor, suddenly merge into one again. In one case, Escharella variabilis, Verrill, I have seen three rows thus merge into one at the margin, suggesting the existence of a *samknopp* (common bud) in the sense of Smitt ('65, pp. 5–16). Ostroumoff ('86^a, pp. 338, 339) has observed a case in Lepralia Pallasiana. He says: "Dans quelques cas, qu'on peut considérer comme des anomalies, il arrive parfois que deux bourgeons, provenant de loges différentes, viennent à se fusionner." It seems to me, therefore, that while Nitsche ('71, pp. 445, 446), who opposed with such vehemence and success the idea of Smitt that zoœcia arise from an undivided marginal zone of cells, was quite right in affirming ('71, p. 447) that even the smallest marginal zoœcia are sharply marked off from the adjacent ones, yet he overlooked the possibility that under certain circumstances the lateral walls might fail to develop, and thus one zoœcium might arise in the place of two, or even three.

I have not read Smitt's Swedish paper, but I do not find anything in the translation given by Nitsche to warrant the latter's conclusion ('71, p. 446) that Smitt believed the "Gesammtknospe" to be "formed from the sum total of the mature peripheral zoœcia." If I understand Smitt, he conceived the *samknopp* not to be derived from the most peripheral mature zoœcia, but to be self-proliferating, and to give rise to the rows of zoœcia, not to arise from them. It is the "bud of the colony," not the sum of the buds of the peripheral individuals of the stock. In this I would agree with him exactly. Although *usually* one finds the marginal gemmiparous tissue forming the lateral walls at the extreme edge of the corm, and thus apparently separated into wholly distinct adjacent gemmiparous masses; under certain conditions, the lateral wall may not be formed between two or more rows, which will then merge into one.

2. Origin and Development of the Individual.

My studies on this subject, which were undertaken for the purpose of showing the unity of the type of budding throughout Ectoprocta, have been very fragmentary.

Figure 72 (Plate IX.) has been introduced for the sake of orientation. It represents a longitudinal vertical section through the peripheral part of a stock of Lepralia Pallasiana. The body wall is thicker at the margin (*marg.*), and gradually becomes thinner as one passes backward. A septum (*sep.*) has already arisen cutting off the youngest zoœcium from the more proximal one, which contains a young polypide; proximal to this is another septum, and the distal end of a third zoœcium.

Nitsche ('71, pp. 445–456) has already well described the process of forming the *zoœcium* in Flustra membranacea. In fact, he has studied the organogeny more thoroughly in many respects than I have. Nitsche ('71, p. 452) showed that the wall of the advancing margin of the colony was composed of two layers of cells, — an outer, "Cylinderepithelschicht," which secretes a cuticula, and an inner, "Spindelzellschicht mit anliegenden Körnerhaufen." As the body wall formed directly from these cell layers is left behind by the advance of the margin, it becomes continually thinner. "Die Cylinderepithelzellen der Wandung platten sich weiter nach dem proximalen Ende zu ein wenig ab, besonders die der Unterseite verkürzen sich, die einzelnen Zellen rücken auseinander, die Zellgrenzen werden undeutlicher, die Kerne jedoch bleiben deutlich erkennbar." Vigelius ('84, p. 76) could not find the inner cell layer in Flustra, even at the youngest stages, and consequently he believed that only one existed at the margin, and that this went to form the "*Parenchymgewebe*" of the adult. Ostroumoff ('86^a, p. 336) seems inclined to doubt the existence of any mesodermal *layer* at the distal portion of the budding zoœcium in Cheilostomes, and Seeliger ('90, p. 580) has failed to find in Bugula "eine *zusammenhängende* dem Ectoderm dicht anliegende Schicht von mesodermalen Spindelzellen." Both Ostroumoff and Seeliger, however, believe in the existence of *isolated* mesodermal elements at the budding end.

According to my own observations, there is usually only one continuous layer at the budding margin of the stock. Thus, in Flustrella (Plate IX. Fig. 79) one can usually distinguish a continuous ectoderm, but the mesoderm (*ms'drm.*) is represented by scattered cells only. At the margin in Lepralia (Fig. 73) one finds a thick ectodermal layer, composed of columnar cells, but the mesoderm consists of an irregular thick mass of cells, some of which appear to be amœboid. They however show no signs of having been derived from the outer layer. The condition of the budding margin of Escharella resembles that of Lepralia. In older parts of the body wall, where the ectoderm is reduced to an extremely thin layer, only scattered mesodermal cells appear, and these are amœboid or mesenchymatoid.

On the other hand, one finds in the body wall, around the nascent neck of the polypide (Plate X. Fig. 88), even to a late stage, both ectoderm and mesoderm well formed as *layers*. The ectoderm is a columnar epithelium; the mesoderm is flatter, and often its cells are not sharply delimited from one another. It is thus perfectly evident, to my mind, that the mesoderm has in general lost its original epithelial character in the marine Bryozoa, although it has retained it in Phylactolæmata. Whenever it does exist in the former group as an epithelium, it is at the budding regions (neck of polypide, and Figures 74, 75, 78, 79, *ex.*).

Origin of the Polypide. — There are very few problems in modern morphology, I fancy, the history of whose investigation shows a less satisfactory aspect than that of the origin of the polypide in Gymnolæmata. It is hardly to be wondered, however, that investigators have sought for another interpretation of the process than the most obvious one, because that seemed to oppose many long cherished and wellnigh universally held dogmas. While the first recognition of the animal nature of marine Bryozoa, which we owe to the studies of Bernard de Jussieu in 1742 and John Ellis in 1755, brought with it a knowledge of their colonial nature, yet it was not until much later that the most characteristic part of this process — the formation of the polypide — was clearly observed. Grant ('27, p. 115) and Farre ('37, pp. 400, 409, 415) first described the process by which is formed this complex of organs, and settled once for all the controversy which had sprung up as to whether these animals were truly stock-builders. Under the influence on the one hand of the endosarc theory of Joliet ('77), and on the other hand of the view promulgated by Hatschek ('77), that similar organs in larva and polypide are equivalent as far as regards their origin from the germ layers, the more important papers[1] between '77 and '90 maintained either that the polypide arose independently of the body wall, and secondarily acquired connection with it, or that it had a double origin.

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[1] Excepting those of Barrois, who, from the study of the favorable material presented by metamorphosing larvæ, has persistently maintained the correct interpretation.

To Nitsche ('71, pp. 456–463) belongs the credit of having first described the histological changes in the origin and development of the polypide of marine Bryozoa, particularly with reference to the part which the germ layers play in that process. He says ('71, p. 456): "Die Anlage des Polypids erscheint zunächst als eine Wucherung der Zellschicht der Endocyste in der Mitte der Hinterwand der Knospe, und zwar in dem Winkel, den die Hinterwand mit der oberen Wand macht. Bald ordnen sich die Bestandtheile des regellosen Zellhaufens in zwei deutlich gesonderte Schichten, und wir sehen nun einen rundlichen Körper, bestehend aus einer äusseren einschichtigen Zellschicht, welche sich scharf absetzt gegen die das Innere des Körpers bildenden Zellen."

This stood until a year ago as the most satisfactory description of this process in the adult stock. The appearance within the last year of the two papers of Prouho ('90) and Seeliger ('90) marks a distinct epoch in the advance of our knowledge concerning the origin of the polypide in Gymnolæmata. The paper of Prouho treats of the process in the case of the primary polypide of the metamorphosing larva of Flustrella, that of Seeliger in the case of the young (practically adult) stock of Bugula. According to both authors, the polypide arises from the body wall by an invagination of it, and its two layers are from the first distinct and separate, and go to form the two layers of the adult polypide, and the whole of those two layers. The outer layer of the body wall gives rise to the outer layer of the tentacles and the lining of the alimentary tract, and the inner layer of the body wall gives rise to the mesodermal lining of the polypide. Prouho alone is cognizant of the method of origin of the ganglion, and in addition there are several points of difference between these two authors concerning the development of other organs, to which I shall refer in the proper place. Thus the latest studies have confirmed the assertions of Nitsche, that the polypide arises from a single centre of proliferation of the body wall; they have made an advance in this, that they have shown that the two layers of the bud do not become secondarily differentiated from a single cell mass, but are respectively derived from the two cell layers of the body wall. My own studies have led me to the same conclusion on this point.

Figure 75 (Plate IX.) is a vertical radial section through the margin of an adult Flustrella stock. The ectoderm is relatively thick at the sole (*sol.*) and margin, and very greatly thickened at the point marked *gm.* Here two layers, sharply separated, are apparent. The cells of the outer layer are columnar and full of granular protoplasm, the mesodermal cells cuboid. The body wall has clearly begun to invaginate in this region. Figure 79 is a similar section, and shows a later stage in this process. The lumen of the bud is apparent, and has been formed by invagination, not, as in Paludicella or Phylactolæmata, by ingression. The two layers of the bud are apparent; they have been derived from those of the body wall.

Figure 73 (Plate IX.) shows a stage in the development of the polypide which is intermediate between that of Figures 75 and 79, but from another suborder, Cheilostomata. The mesoderm has here a mesenchymatous character, and is loosely attached to the inner layer of the bud; it is not always sharply marked off from it by boundaries, but is quite distinct in its reaction with staining reagents. This bud has evidently arisen by invagination of the body wall. Seeliger ('90, p. 581) also finds that there is an actual invagination of the ectoderm in Bugula, the opening to which he calls "blastopore."

From what has been already shown, it is evident that in Flustrella, as well as in Cheilostomata, the first appearance of the young polypide is near the margin of the stock, not near the proximal part of the young zoœcium. This will also be apparent at 6 and 9, Figure 71 (Plate VIII.), where the accumulation of nuclei immediately behind the margin indicates the neck of the polypide, — the point at which the bud arose. To be sure, at quite an early stage, but very much later than that of Figure 73, the polypides are found near the proximal wall of the zoœcium, but a delicate funnel-shaped sheath of tissue runs from the polypide to the distal part of the zoœcium, where the polypide is attached to the body wall.

After invagination the pocket closes at its attached end by a growing together of its lips (Figs. 79, 78). Thus the body wall becomes continuous again over the lumen of the bud, and this union is first broken when the fully formed polypide is ready to evaginate itself. Seeliger ('90, p. 582, Taf. XXVI. Figs. 8, 10) has described and figured a similar condition in Bugula.

The young bud now becomes elongated (Fig. 80), the walls of the bud sometimes becoming closely approximated. A little later it begins to pass backwards relatively to the distal wall of the zoœcium. A transverse section through the young polypide and the neck of the colony shows that the connection has become a less intimate one (Fig. 81, *cev. pyd.*). The tissue by which the connection is still effected is that from which the kamptoderm will be formed. It is apparently the existence of this stage, in which the kamptoderm is long drawn out and easily overlooked in optical as well as actual sections, that led to the belief that polypide buds may arise independently of the body wall and only secondarily become connected with it.

At about this time the lumen of the *alimentary tract* begins to be separated from that of the atrium. Thus, in the series from which Figure 81 was taken the more oralward lying sections show that the cavities of the lower and the upper parts of the bud, which at the anal end are broadly confluent, have here become separated by a constriction. A sagittal section of a somewhat later stage is shown in Figure 76, which is from Flustrella. Here we find the alimentary tract represented by a space in the lower part of the bud, broader at its anal than at its oral end and separated from the upper cavity — the common atrio-pharyngeal cavity, *œ.* + *atr.* — by a line of nuclei which represents the line of approximation of the inner layers of the two sides of the bud. The bud is attached to the body wall at its marginal (anal) end, and is free from it oralwards. (Compare with Paludicella, Plate III. Fig. 24.) It seems to me highly probable from these and other series of sections that the alimentary tract is separated from the rest of the lumen of the bud, not by an approximation of the inner layers of the bud along the whole extent of the future alimentary tract at once, but that the rectal part is first formed and constitutes a large cavity, at first broadly open to the atrium above, and that the gastric portion is formed somewhat later by a progressive enlargement of the lower cavity of the bud, which now becomes constricted off from the atrium and œsophagus above. This process is like that found in Paludicella (page 19), which forms a sort of transition to that of Phylactolæmata, described by Braem ('90, pp. 45, 46) and myself ('90, p. 112).

Prouho ('90, p. 448, Fig. 6) shows that the rectum at first appears as a *blind sac* open to the atrium at its posterior end, although later this opening is greatly reduced. Hence in the Flustrella larva also the space from which the lumen of the future rectum is to arise is formed before that of the stomach, although this part of the alimentary tract is the last to be cut off from the atrium. Seeliger ('90, p. 585) says concerning the formation of the alimentary tract in Bugula : "Der ganze Basaltheil des Polypids sich in der Mittelpartie durch zwei immer tiefer werdende Furchen von dem vorderen abschnürt, während er an zwei Stellen, einer oberen und einer unteren, mit ihm in Verbindung bleibt. Die obere Verbindung entspricht dem Anus, die untere dem Mund." The author here seems to imply that the whole alimentary tract is formed at one time; but as he has not attended particularly to this point, this can hardly be said to militate against my view.

There is, however, in my opinion, a more important error in Seeliger's description of the origin of the alimentary tract, — an error into which Nitsche ('71, p. 457) also fell. As in Phylactolæmata and Paludicella, so also in marine Bryozoa in general, so far as I have studied them, the posterior and anterior parts of the alimentary tract are formed independently, and their cavities coalesce only secondarily. The constriction which separates the lumen of the bud into a cavity nearer, "*vorder*," and one more remote from the body wall, "*basal*," does not separate off the whole alimentary tract from the atrium. Neither does that constriction result in the formation of a space opening into the cavity nearer the body wall, "*Vordertheil*," at an upper [distal] point (anus) and lower [proximal] point (mouth). Thus if one examines a complete series of sections through a polypide even of so late a stage as Figure 92 (Plate X.), one finds that, while there is an open connection between the anal end of the alimentary tract and the atrium, the oral end is at all points sharply separated from the cavity above by a double-layered wall of cells, as is shown in Figure 92, between *œ.* and *ga.* Such a condition, moreover, has been found by Barrois ('86, pp. 73–76) in the primary polypide of Lepralia, and by Prouho, as just stated, in the primary polypide of Flustrella.

Origin and Development of the Ring Canal and Tentacles. — Nitsche ('71, p. 430) first described in Flustra a ring canal surrounding the mouth-opening and lying at the base of the tentacles, but did not refer to the origin of it. Seeliger ('90, p. 588) describes it in a young polypide of Bugula, as derived from the mesodermal layer.

My own sections also show that it arises on each side of the œsophagus as a groove lined by mesoderm (Plate X. Fig. 92, right). This canal, which is shown cut along its course in Plate IX. Fig. 82, *can. crc.*, is not wholly separated from the body cavity, but communicates with it below the brain. This communication occurs in the section below that shown in Figure 82, near the point *can. crc.* This ring canal at an earlier stage is shown in Figure 87. It has not yet been formed backwards nearly so far as the brain; anteriorly the section has traversed the tentacles under which it runs. The canal is also shown cut across in Figure 86 at the base of a tentacle, with whose lumen its cavity is directly continuous.

The formation of the tentacles is closely connected with that of the ring canal, from the upper wall of which they arise. Since the upper wall of the ring canal is two-layered, the tentacles are two-layered also. The outer layer of the tentacle is thus derived from the inner layer of the bud; the inner layer, on the contrary, from the outer layer of the bud. It would be hardly necessary to make this statement, which agrees both with early and the most recent observations, had not Barrois ('86, p. 75, Fig. 48) referred to and figured the tentacles as having been formed from the inner layer of the bud *only*.

My observations fully confirm Seeliger's ('90, p. 587) description of the manner of growth of the tentacles; that is, that the outer edge of the ring canal, together with its tentacles, moves downward and outward along the sides of the polypide, turning the axis of the tentacle from a nearly horizontal to a vertical position, and increasing the area of the kamptoderm. Thus in Figure 92 this process has progressed farther on the left side than it has on the right.

Nitsche ('71, p. 458) lays some stress upon the statement that the tentacles are not at first few in number, gradually becoming more numerous; on the contrary, he says, "Ich sah stets, beim ersten Auftreten von Tentakelanlagen, 16, 17, oder 18 Stück gleichtzeitig erscheinen." Seeliger ('90, p. 584) agrees with Nitsche in this respect; but Prouho ('90, p. 449) finds the conditions different in Flustrella. Here the tentacles "ne se développent pas simultanément sur tout son pourtour, mais apparaissent d'abord de chaque côté du plan de symétrie, puis se multiplient vers l'arrière." As I have shown, 14 of the 17 tentacles arise nearly simultaneously in Paludicella, for here there are few of them; and this is the case also in Escharella variabilis with its 17 tentacles.

As the tentacles of both Flustra and Bugula are few in number,[1] the statements may easily be considered to be correct for these genera. The tentacles of Flustrella hispida are much more numerous (30–35), and Prouho's statement may well be true for his form. In fact, my own observations on this species are fully in accord with those of Prouho. Figure 77 (Plate IX.) represents a young polypide of a Flustrella corm, viewed from the roof as an opaque object. Six tentacles were visible on each side of the bud, but the oral and anal parts of the corona were yet incomplete. The remaining nine or ten pairs of tentacles subsequently arise oralward and analward of these rudiments.

Much disagreement has prevailed concerning the number of layers involved in the *kamptoderm* of marine Gymnolæmata, in both the adult and the developmental stages. As in so many other cases, we owe to

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[1] Bugula avicularia has 14 or 15 tentacles, and Flustra (Membranipora) membranacea 20, according to Hincks ('80, pp. 76 and 140).

Nitsche ('71, pp. 431, 432) our first intimate knowledge of this organ. He believed it to consist in the adult of Flustra of a single cell layer, in which are imbedded (or applied?) longitudinal and circular muscle fibres. He believed the kamptoderm to be formed gemmigenetically only by the outer cell layer, the derivative of the mesoderm. Repiachoff ('75, pp. 138, 139) observed in Tendra (Membranipora) "die Doppelschichtigkeit der Tentakelscheide nicht nur bei den jungen Knospe sondern auch bei den ganz ausgewachsenen, offenbar schon längst functionirenden, in ihrem mittleren Theile ganz braunen 'Polypiden,'" and later ('76, p. 152) a similar two-layered condition of the kamptoderm (Tentakelscheide) in Membranipora and Lepralia. Ehlers ('76, p. 37) finds a single layer of cells in the kamptoderm of the adult Hypophorella (Ctenostome), which he believes is continuous with the endocyst of the body wall, and thus is ectodermal. He finds neither longitudinal nor circular muscle fibres. Haddon ('83, p. 517) believes the kamptoderm to be derived from both the inner and outer layer of the polypide bud. Vigelius ('84, pp. 33, 82) describes it as arising from the mesoderm only (Parenchymegewebe), and as being essentially one-layered, both longitudinal and circular muscles lying in this layer. Barrois ('86, p. 74) derives the kamptoderm from the mesodermal layer only. Ostroumoff ('86^a, p. 15) believes the kamptoderm to be two-layered and provided with muscles; it is in his opinion derived from both layers of the bud. Freese ('88, pp. 18, 19) studied only the adult of Membranipora. He admits the presence of muscle fibres, but believes the kamptoderm one-layered. Pergens ('89, p. 507) states only that in the Cheilostomes studied by him the tissue of the kamptoderm is composed "aus abgeplatteten Zellen, zwischen welchen Längs- und Ringmuskelfasern eingebettet sind." Prouho ('90, p. 451) states that in the primary polypide of Flustrella this organ is early differentiated, "et les deux couches de rudiment prennent part à sa formation." Finally, Seeliger ('90, p. 587): "Es kann danach keinem Zweifel unterliegen, dass die Tentakelscheide ektodermalen Ursprungs ist. . . . Das Mesoderm erscheint auf allen gelungenen Schnitten von der Tentakelscheide scharf abgesetzt."

It is my belief that throughout the group of marine Gymnolæmata, as in Paludicella and Phylactolæmata, the kamptoderm is derived from both of the two layers of the polypide bud, is provided with a strong system of longitudinal and a slight one of circular muscles, and contains in the adult two layers, or at least modified representatives of two layers. I have arrived at this conclusion from a careful study by sections of the following genera: Bugula, Lepralia, Escharella, Flustrella, Bowerbankia, and Crisia. The existence of two layers was easily demonstrated in all cases in the young polypide by cross sections of the "neck." The two layers are of nearly the same thickness, and distinctly separated from each other. The presence of two layers in the adult is more difficult to determine, but it was always indicated by the occasional presence of two nuclei lying side by side, and especially at the attachment to the diaphragm. The presence of muscles was demonstrated in all cases (except Bowerbankia, where my few sections did not show the proper region) upon tangential sections of the sheath. I may add, that the existence of muscles is wellnigh conclusive *a priori* evidence of the existence of the mesodermal layer, since nowhere else in Bryozoa, so far as I know, do muscles arise from any other layer. Prouho's evidence in support of his position is perfectly satisfactory to my mind, certainly more so than the negative evidence of Seeliger in support of his. In further support of my statements I may refer to the condition of the kamptoderm (*kmp'drm.*) in Figures 92 and 83, Plate X.

Nervous System. — Since Dumortier discovered, in 1835, a ganglion in Lophopus, there has been seen in marine as well as fresh water Bryozoa a body which has been considered, with greater or less certainty, to constitute the central nervous system. Overlooked by Farre, it was, I believe, first described for marine Gymnolæmata in 1845 by van Beneden, co-worker with Dumortier, for Laguncula (Farrella). Nevertheless, up to the present the evidence of its being a ganglion homologous with that of Phylactolæmata has not been satisfactory. The homology can be established only by determining its similar origin with the brain of Phylactolæmata; its function can be best established by showing the existence of ganglionic cells and fibres. I hope to have advanced our knowledge in both of these directions.

At about the time that the œsophagus and stomach have become confluent, one notices a papilla-like elevation of the floor of the atrio-pharyngeal cavity. This has been noticed by Korotneff ('74) in Paludicella, and by Nitsche ('71, p. 459) and Seeliger ('90, p. 586) in Cheilostomes. It has been called by them "Epistome," and compared with that of Endoprocta or Phylactolæmata. In my own opinion, it is merely a structure brought into prominence by the sinking down of the floor behind it to form the ganglion (Plate X. Fig. 86, *gn.*). This depression has been seen by Barrois ('86, pp. 74, 75) and Prouho ('90, p. 450), and rightly interpreted by them as probably destined to give rise to the central nervous system. That this is the correct interpretation is shown by later stages from different species, as Figures 89 and 83, in which we see the ganglion gradually assuming the position it has in the adult, on the anal side of the pharynx at the base of the anal tentacles.

A section across the pharynx in such a stage as Figure 83 is shown in Figure 87. A comparison with Figure 51 (Plate V.) of my Cristatella paper (Davenport, '90) will show a great similarity of conditions at about the same age, and can leave no doubt concerning the homology of the regions marked in both cases *lu. gm.*; or compare Taf. VIII. Fig. 100, *nh.*, of Braem's ('90) magnificent work. A section through a later stage is shown in Figure 82. The brain has already sent out circumœsophageal nerves, as in Paludicella. The central part of the ganglion does not stain; one sees only a granular mass, sometimes with signs of short fibres. In the cornua (*n'*) one occasionally sees very large clear nuclei with a single nucleolus, lying in the midst of a cell mass which is spindle-shaped and stains more deeply than adjacent cells. These remind one strongly of bipolar ganglionic cells, but fibres could not be traced far from their pointed ends. Series of sections of Flustrella parallel to Figure 82 show, as one passes below the level of the ganglion, a continuous band of cells extending down from it towards the cardiac valve and between the cell layer lining the œsophagus and the surrounding mesoderm. One is reminded of the exactly similar conditions in Paludicella (page 26), and of the "linienartige Zeichnung" seen by Nitsche ('71, p. 431) and Vigelius ('84, p. 42) in the same place in Flustra. These facts go to indicate the existence of a gastric nerve.

At about the time at which the ganglion arises, the cavities of the stomach and the œsophagus become confluent (Fig. 86 *œ.*). At this stage (somewhat earlier than Figure 86) the alimentary tract consists of a U-shaped tube of nearly uniform calibre, and without any indication of the cœcum. The tentacles lie in two parallel rows in the middle of the bud, the corona being incomplete both in front and behind, but less so oralwards than towards the anus (Fig. 77, *atr.*). In fact, while new tentacles are formed later towards the oral median line, they never appear behind the line *atr.* This hinder region has another fate. Its wall increases very greatly in area, diminishes correspondingly in thickness, and forms a large part of the kamptoderm lying behind the postoral tentacle in Figure 86. With this growth of the kamptoderm the anus is carried backwards, and farther and farther from the posterior ends of the rows of tentacles, immediately behind which it formerly lay.

As the kamptoderm grows in area, the polypide comes to lie in the proximal part of the zoœcium. *Pari passu* with this process occurs the *rotation of the oral tentacles*, as in Paludicella. The oral tentacles which at first lie perpendicular to the roof of the colony (Fig. 86) gradually come to lie parallel with it (Figs. 89 and 83). The œsophagus loses its elongated, laterally compressed form, and becomes circular, and the ganglion lies just below the mouth-opening. Not until now, in fact, can one speak of a mouth. It was not at all formed synchronously with the anus. To illustrate this process I have taken three different genera representing different stages. Similar stages could have been obtained from each genus. By using three genera, the similarities as well as the dissimilarities of the process are indicated. Among other things, the larger size of the polypide and shorter kamptoderm of the Ctenostome Flustrella (Fig. 89) is noticeable.

Lastly, the cœcum is formed as a wholly secondary differentiation of the alimentary tract. This arises in some species relatively earlier than in others; thus it is better developed in Figure 86 than in the later stage of Figure 83.

The lining cells of the alimentary tract now rapidly undergo the differentiations characteristic of the different regions. The most extreme modification takes place in the *pharynx*. In Cheilostomes the cells of this region gradually become vacuolated, until finally very little stainable protoplasma remains. The nucleus lies at the deep end of the cells. A very peculiar modification of the cell walls takes place, in that they become plainly perforated by holes through which the adjacent cells are in communication (Fig. 85). It is in a region similar to this that the cells become cuticularized in Bowerbankia to form the so-called gizzard. The pharyngeo-œsophageal region is also provided with a very powerful musculature of circular muscles (*mu.*, Figs. 85, 86).

Concerning the *origin of the muscles* I have made very few studies. The parieto-vaginal muscles seem to arise, as in Paludicella, from around the neck of the polypide, and the retractors from the oral end of the polypide bud (*mu. ret.*, Fig. 89).

The *neck of the polypide* sinks below the general level of the body wall by an infolding of the latter, as described for Paludicella, and the mass of columnar cells which passes down with it forms, I am confident, the *diaphragma* of Nitsche ('71, p. 432), which is thus exactly comparable with the mass of cells around the atrial opening of Paludicella in Figure 45, *of. atr.* (Plate V.). According to this view, then, the diaphragma is not placed at about the middle of the kamptoderm, but at its proximal end, and all that lies between it and the outer body wall — the non-evaginable portion — has been formed in the elongated neck, exactly as the non-evaginable portion is formed in Phylactolæmata (see

Davenport, '90, Plate IX. Fig. 77, Plate XI. Fig. 98) and Paludicella (Plate V. Figs. 50 and 45).

As my purpose is not so much to present a complete organogeny of Bryozoa as to show the method of origin of the bud and the fate of the layers, I have had to desist from carrying on my studies further in the organography, and have left many interesting and important questions unsolved; such, for instance, as the development and structure of avicularia, the presence of an excretory system, and the degenerative processes which occur with regularity in the polypides.

3. Regeneration of the Polypide.

I have been led to study the regeneration of the polypide because Ostroumoff seems to believe that in regenerating buds the digestive epithelium of the stomach is derived from an extraneous source, — the brown body. Thus he says ('86ª, p. 340) the brown body appears as a cœcal appendage of the young digestive tube. "C'est sur ce dernier [tube digestif] qu'on trouve un groupe de cellules affectant la forme d'un bonnet et se réunissant très tôt à l'angle proximal du rudiment ectodermique. A mesure que les cellules du bonnet, ainsi que la masse brune, sont employées à la formation de la portion moyenne du tube digestif, ces dernières se débarrassent de leur contenu," etc.

The external phenomena of regeneration are well known. In the Membranipora stock, for instance, one sees polypides being produced at the margin, and one finds them older and older as one passes backwards, until finally they are seen to be wholly degenerate, and to be replaced by young polypides. Thus, in passing backward along a single row of individuals in a Membranipora stock about 18 mm. long, I have seen this process of regeneration recurring four times. In Alcyonidiun, too, one finds an apparently regularly recurring degeneration and regeneration of polypides. In the mat-like Cheilostomata the regenerating polypide (Plate VIII. Fig. 71, *pyd. rgn.*) is always found at one place, — namely, on the operculum, — that is, proximal of the opercular opening.[1] In Flustrella it is found in a similar position on the dorsal body wall, proximal of the cuticularized introverted portion. My studies have been chiefly made on the Cheilostomata. Figure 91 (Plate X.) represents an early stage in the formation of a regenerating polypide. Here, as in the marginal polypides, there is a typical invagination involving the two layers of the body wall (*i.*, *ex.*). Owing to the reagent, the body wall is shrunken from its contact with the operculum (*op.*).

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[1] Haddon ('83, pp. 522, 523) has found the regenerating polypide arising from the same place in Flustra membranacea and in Eucratea, and Ostroumoff ('86ª, p 339) in Cheilostomes in general.

If one inquires what has been the histological conditions of this region antecedent to this stage, one must look to younger adjacent and marginal zoœcia, since they reproduce these conditions. I will again call attention to Figure 88, which represents a cross section of the body wall through the region of attachment of the kamptoderm of a young polypide of about the stage of Figure 83. This, then, represents the neck of the polypide, and it is from about this region that the operculum and finally the regenerating polypides will arise. The cells are columnar, and stain deeply about the nuclei, and both cell layers are well developed. Elsewhere in this same individual the body wall is composed of smaller, flatter cells, and two layers are not easily distinguished. The region of the future operculum possesses at an early stage some of the largest, most columnar cells of the body wall. The cells of this region do not, however, retain their peculiarly large size throughout life, but in the adult we find the same region occupied by a flat epithelium, nearly as thin as the epithelium shown in Figure 90. Meanwhile the epithelium of the rest of the body wall has become still more attenuated. The difference between the body wall of the operculum and that of adjacent regions is best shown by the greater abundance of nuclei under the opercular region when the stained stock is looked at *in toto* from the roof (Plate VIII. Fig. 71). The regions of the future opercula are seen, in young zoœcia (Fig. 71, *4*, *6*), to be patches of densely packed nuclei. The opercula of older zoœcia show a slight preponderance of nuclei, and thus indicate more numerous cells. It is from such a region, then, that the young regenerating polypide arises.

As in the case of the marginal polypides, so here, the lips of the invagination pocket close and become fused to form the neck of the polypide (Plate X. Fig. 84). The later stages of the development of the regenerating polypides seem to be the same as those of the marginal buds. Figures 74 and 89 are, indeed, regenerating polypides. I cannot find any evidence that the alimentary tract, or any part of it, is formed in regenerating buds by a method differing in any essential particular from that in marginal buds.

It is well known, however, that the degenerated polypide which forms a "brown body" in the old zoœcium eventually disappears. Haddon ('83, p. 519) maintains that in the developing regenerated polypide "the walls of the stomach, or, more strictly, that portion of the stomach which forms the gastric cœcum, grow round and envelop the brown body, so that the brown body passes as a whole into the alimentary tract of the young Flustra." It seems to me that the burden of proof of such a remarkable occurrence lies with him who asserts its existence, and certainly sufficient evidence is not presented by Haddon.

To settle this question in my own mind, I cut a series of thin sections through a part of a stock of Escharella (which in budding shows a practical identity with Flustra), in which all stages of regenerating polypides were to be found. From complete series, at critical ages, I utterly failed to find any indication of the inclusion *in toto* of the brown mass by the polypide. But I found the alimentary tract of the polypides usually applied to the brown body (*pyd. dgn.*), as shown in Figure 92. At this stage the degenerated mass is surrounded by spindle-shaped cells, and just within these by a homogeneous or lamellated sheath. At later stages the elements of the degenerated mass were seen to be more loosely associated. The cells of the alimentary tract at the same time appear highly granular, and a granular coagulum often partly fills the alimentary tract. Before the new polypide is ready to expand itself, the brown body as such has often wholly disappeared. Just as my sections leave no chance for the brown body to be included *en masse* by the alimentary tract, so too do they yield no evidence of the addition to the latter of new cells from this degenerate mass, as Ostroumoff, in the sentence quoted above, implies.

The interesting facts of degeneration in Bryozoa deserve a more careful study than I have been able to give them. We are quite ignorant of the physiological significance of the regularly recurring degeneration and regeneration in certain Bryozoan colonies. Ostroumoff ('86^a, p. 339) has offered an interesting hypothesis, to the effect that the degeneration of the polypides, the remains of which are taken into the stomach of the regenerated polypide and the undigested portion of which is cast out with the fæces, is a method of excretion, made necessary to these animals from lack of urinary tubules.

IV. Origin of the Gemmiparous Tissue in Phylactolæmata.

After having found that in Paludicella and the marine Bryozoa, as in Phylactolæmata, the growth of the colony takes place at the margin or tips, and that it is here primarily that buds originate, and after having thus found that throughout the group all of the organs of the polypide are derived from two layers, of which the inner gives rise to organs so dissimilar in origin as the central nervous system and the alimentary tract usually are, it becomes a matter of no little importance to solve the two problems, what is the origin of these growing regions, and what that of the two layers. Through the works of Barrois ('86), Ostroumoff ('87), Vigelius ('88), and especially Prouho ('90), on the metamorphosis of the larva and formation of the first polypide of Gymnolæmata we are fairly well acquainted with the facts in this group; but a careful study has not heretofore been made of the Phylactolæmata with reference to the points mentioned above. Korotneff ('89) and Jullien ('90) have published quite extensive papers on the ontogeny of Phylactolæmata, which describe too incompletely the stages which should reveal the required facts.

In order to throw a little light on these questions, I undertook the study of the embryology of two species of Phylactolæmata. But before beginning the account of what I have found, it is necessary to remind the reader of some facts concerning the origin of the polypides in the adult colonies. For our knowledge of these we are chiefly indebted to Braem ('90, pp. 18–32) ; it has also been my privilege to confirm many of them.

The details of the budding process are slightly different in Plumatella and Cristatella. In the latter genus the body wall becomes highly modified as it grows older by the formation of secreted masses which nearly fill most of the ectodermal cells. In Plumatella, on the contrary, the ectodermal cells retain, for the most part, a more primitive, unmodified condition. Here, moreover, by a rapid growth at the neck of the polypides, the individuals are carried to considerable distances from one another, whereas in Cristatella there is a less rapid growth resulting in a compact stock.

In Plumatella, the whole of the embryonic tissue from which any bud arises does not go to the formation of a polypide, but a part of it remains as the neck of the polypide, and gives rise by cell proliferation to the body wall and the *Anlage* of a new bud. Thus the *Anlage* of each bud is part of that of a preceding bud. The question remains yet unsolved, Whence came the *Anlage* of the first polypide? Since the embryonic tissue of the inner layer of the bud, which seems to take the most active part in the formation of the bud, gives rise to both the lining of the alimentary tract and the wall of the brain, it becomes an exceedingly interesting question, From what germ layer is this inner bud layer derived?

In Cristatella, as in Plumatella, not all of the embryonic tissue from which any bud arises goes to form that bud; but some of it is, apparently, passed along under the highly metamorphosed cells of the ectoderm, again to divide itself, one part going to form a new polypide, the other to form the *Anlagen* of new buds. In Cristatella, this embryonic mass of cells of the inner layer of the bud seems to be to a considerable extent independent of the highly metamorphosed ectoderm, and to form at places a sort of third layer, lying below the true ectoderm and above the muscularis with the cœlomic epithelium. Here, too, while it is easy to see buds arise from preceding buds in the adult colony, we cannot consider our question answered until we have discovered the origin of the cells from which, as from a stolon, the *Anlagen* of polypides successively arise.

I desire to say that I have avoided giving a full account of the ontogeny of these species, both because it is not directly required for the solution of the problems in hand, and because we are promised studies in this field by Braem.

The eggs of Phylactolæmata arise, as has long been affirmed, from the cœlomic epithelium of the body wall. The evidence of this is conclusive, for one often sees in a single section various stages in the development of the eggs. (Plate XI. Fig. 93, *ov'*.) It is also to be observed that they do not arise indiscriminately from any region of the body wall, but always close to the neck of a polypide. Sooner or later these eggs, surrounded it may be by a few follicular cells, are enclosed in an oœcium, and here undergo their development up to the stage of a young stock, possessing perhaps a dozen immature polypides. In the figures on Plates XI. and XII. the oœcium (*oœ.*) has been usually drawn, but in Figures 100 and 104 it has been omitted. As a result of cleavage, a blastula is formed, and from one pole of this — *the pole nearest to the neck of the oœcium* — cells are given off which move into the blastocœl (Figs. 94, 98) and finally come to line the cavity. It is important to observe that in the earliest stage of this process found there were four inner cells, of which two are represented in the section (Fig. 94, *ms'drm.* + *en'drm.*). Thus the two layers of the adult body wall are established. Up to this stage the conditions are practically the same in Cristatella and Plumatella. From now on, they are somewhat different in the two genera.

The first difference to be noticed is in the oœcium itself. In Cristatella the cells composing this rapidly become a pavement epithelium (Fig. 97); in Plumatella, on the contrary, the cells of the oœcium remain columnar (Fig. 99). The neck of the oœcium also differs in the two cases. In Cristatella it is long, thick, and filled with a dense mass of large cells (Figs. 95, *cev. oœ.*, and 101 *, 102 *). In Plumatella (Fig. 99) it is very short.

The second difference concerns the embryo itself, and is connected with the formation of the first polypide. In Plumatella (Fig. 99) the first indication of the formation of the first polypide occurs at or very near the neck of the oœcium, or, since the ingression of cells into the blastocœl took place at the pole of the blastula nearest the neck, we may say near to the pole at which ingression occurred. The cells of the outer layer (*i.*) are elongated and contain large ellipsoidal nuclei which are often pressed close together. All of the cells of the larva stain more deeply at this pole than elsewhere, and those of the inner layer rather more deeply than those of the outer. The nuclei are also very large, those of the outer layer being possibly more prominent than those of the inner; but the difference is not so marked as in the drawing, where too the nucleoli of the inner layer are represented relatively too small. Even at this stage one finds in another section of the same embryo the beginning of a second polypide, whose position is indicated at *. This second polypide is indicated merely by a considerably thickened inner larval layer, and a very slightly thickened outer one. The two polypides are thus seen to be wholly independent of each other. The first invagination further advanced is seen in cross section of the whole larva in Figure 96. The entire outer layer would seem at first sight to be involved in this invagination; but even in this figure there are seen one or two nuclei which lie under the oœcium at the place of invagination. I believe that they will not be involved in it, for at a very little later stage (Fig. 104) one finds a layer of cells lying over the invaginated bud, which I believe are destined to form the ectoderm of the body wall at this place.

Later stages in the development of the larva in this species are not shown. The bud follows, I am confident, the same steps that are pursued by the bud in the adult colony. A placenta-like connection of the larva with the oœcium, which was first described by Korotneff ('87, p. 194), begins at about this stage, and continues until two well formed polypides are present. This "gürtelformige Placenta" begins to form in about the middle of the young embryo, and the elongated cell of the outer layer of the larva, in contact with the oœcium shown on the left of Figure 99 below the *, is, I believe, the first indication of it. The oœcium and larva both continue to increase in size, and the walls of the former become thinner with their increase in area.

The attachment of the oœcium to the body wall of the mother stock always remains small, as in Figure 99, and the embryo, in my experience, does not come in contact with it.

The formation of the first polypide in *Cristatella* is preceded by another process. Just as in the adult colony the inner layer of the polypide does not arise by invagination of the ectoderm, but from the stolonic cells lying at the base of the ectoderm (see Davenport, '90, pp. 108, 109, Figs. 4 and 15), so too in the embryo. The first process then must be the formation of the stolonic cells. Figure 101 shows at the point marked *sto.* (which is at the pole of the embryo whence the inner-layer cells originated) that certain of the cells of the ectoderm appear to be arching over a disk, containing about six cells in section, and thus coming in contact with the cylinder of cells (*) which projects from the neck of the oœcium. By a continuation of this process, the central disk of cells gradually comes to lie below the general level of the ectoderm, and to be cut off from contact with the neck of the oœcium (Fig. 97, *sto.*). The position of the stolonic mass with reference to the neck of the polypide in this last figure must be considered abnormal; it is at any rate exceptional, as it lies at one side of the neck of the oœcium, which does not, therefore, appear in this section. The next later stage which I have found is shown in Figure 102. The stolonic mass seen lying beneath the ectoderm in Figure 97 has here already given rise to a young polypide (*i., ex.*), and its area is increasing in all directions by cell division (*sto.*). The beginning of a second polypide is indicated on the right at *sto.* The ectoderm is seen lying above this stolonic mass, and closely applied to the neck of the oœcium (*).

Neither at this nor at any subsequent stage have I been able to detect in Cristatella any "gürtelformige Placenta" such as exists in Plumatella. I am therefore of opinion that the process of nutrition, which is effected in Plumatella from the oœcium through its placenta, is effected in the Cristatella larva by its attachment to the neck of the oœcium. I am pleased to see that Jullien ('90, pp. 13, 14) has also reached this conclusion in a paper which he has had the kindness to send me. At a later stage, the embryo, or young colony, seems to become detached from its intimate association with the neck of the oœcium, as we see in Figures 95 and 103.

Figure 103 represents a stage in which there are two well developed buds, both shown in the section. There is, in addition, on another section, one less developed. The stolon is seen passing oralward of these two primary polypides, or rather the primary and secondary one. Moreover, as the series of sections shows, the stolon does not exist merely in this section, but it is a disk which is cut here in one of its diameters. A separation of the stolonic mass has occurred between the two oldest polypides, so that the ectoderm is here in contact with the cœlomic epithelium, just as is the case between buds in the adult stock. As the colony increases, the inner and outer margins of the stolonic tissue continue to extend farther outward, and this tissue forms at first a broad ring of ever increasing diameter. Later, as the area of the stock increases, the ring becomes broken, so that, instead of growing along an infinite number of radii, its growth is confined to a few, as in the adult colony.

I will defer a discussion of the significance of these facts to the general part of this paper.

B. GENERAL CONSIDERATIONS.

I. Laws of Budding.

Carefully conducted studies on stock building have generally revealed, just as these on Bryozoa have shown, a law in budding. This law in budding results in the formation of a stock the interrelation of whose individuals is a determinate one. I now propose to offer an hypothesis to account for the existence of these laws, and then to show how facts of budding in Bryozoa and other groups can be explained by means of it.

And first of all I must acknowledge that this hypothesis, although perhaps here first formulated, really depends upon observations and deductions made long ago on this group, first by Hatschek, who from 1877 has maintained that individuals do not arise independently of one another, and secondly and mostly to Braem, who in '88 (pp. 505, 506) declared of Phylactolæmata "dass in dem Stock keine Knospe entsteht, die nicht auf das embryonale, d. h. den specifischen Leistungen der Körperwand noch nicht angepasste Zellmaterial einer älteren Knospenanlage zurückgienge und dass somit in der ersten Knospe des keimenden Statoblasten sämmtliche Knospen des künftigen Stockes implicite enthalten sind." Not less is the following hypothesis indebted to the ideas of Roux and Fraisse, and to Nussbaum, who has said ('87, p. 293): "Ein lebendes Wesen ist somit als Ganzes oder in seinen Theilen soweit individualisirt und vergänglich, als die Gewebebildung und die Theilung der Arbeit vorgeschritten ist; das Ueberdauern der Einzelexistenz, die Theilbarkeit auf geschlechtlichem oder ungeschlechtlichem Wege, spontan oder künstlich bedingt, ist an das Vorhandensein undifferenzirter Zellen gebunden und ist um so grösser, je weiter im Organismus diese Zellen verbreitet sind"; and, finally, to the idea which is implied in the conclusions of Nussbaum ('80, pp. 106–113) and Weismann, that germplasma does not find its origin in the parent individuals, but is merely borne by them in its unbroken passage from generation to generation.

This hypothesis is simply that *there is in every stock of Bryozoa a mass of indifferent cell material which is derived directly from indifferent cells of the larva or embryo, and whose function is to form the organs of the various individuals, including the polypides.* This indifferent cell material lies in the body wall, principally at the growing tip or margin of the stock. By its growth and differentiation it gives rise to the body wall, muscles, etc., and at intervals it leaves behind, as a portion detached from itself, a mass of indifferent cells, which is capable of forming a polypide, or of becoming a new centre of growth, or of both. Which of these possibilities will be fulfilled, where and when these masses of indifferent cells will be left behind, depends upon the necessities of the species, and the variations in these respects give rise to the peculiar characters of the different stocks.

This hypothesis differs from that of Braem in that the pre-existence of a *Knospenanlage* assumed by Braem is, according to my view, a non-essential feature in the formation of the colony; the pre-existence of an indifferent cell mass, which does not itself constitute buds, but may give rise to masses which can, is the only essential feature.

As a first application of this hypothesis I refer the reader to the conditions of stock formation in *Paludicella,* already described. We find at the tip of the colony a mass of large proliferating cells, which I regard as histologically undifferentiated. These cells give rise to the body wall, — the cystid, — and at intervals leave behind three masses of cells, which I regard, from the fact that they retain their cuboid condition, as well as from their ultimate fate, as indifferent or embryonic. The median mass of each of these gives rise to a polypide, and to one only. The lateral masses form centres of growth similar to the one from which they were derived.

In order to reproduce the arrangement of individuals in the stock resulting from this manner of budding, we may make use of some graphic method of representation, as Smitt ('65ᵃ, pp. 139, 140) did long ago, and as Allman ('70), Semper ('77, pp. 67–78), Chun ('88, pp. 1167–1180), Braem ('90, pp. 33 and 44), Ehlers ('90, p. 9), and others, have since done. I shall represent the mass of indifferent cells by an asterisk, and individuals (according to Chun's nomenclature) by the use of the large and small letters of the Roman alphabet, and, finally, by Greek letters. The typical stock of *Paludicella* might then be graphically represented thus (cf. Plate I. Figs. 2 and 2^a) : —

```
                                                *
                                              * c *
                                              *   *
                                            * a b a *
                                *             *   *
                              * b *         * *   * *
                              *   *       * β a a a β *
                  *         * a a a *       * *   * *
         *      * a *       *   *
(1)     * D       C           B               A
         *      * a *       *   *
                  *         * a a a *       * *   * *
                              *   *       * β a a a β *
                              * b *         * *   * *
                                *             *   *
                                            * a b a *
                                              *   *
                                              * c *
                                                *
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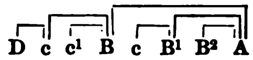
Here the letters indicate polypides or their *Anlagen*, and the asterisks indifferent tissue. The individuals represented by capital letters may be called primary individuals; they may be said to belong to the primary series, and to have been derived from the primary indifferent mass. The individuals represented by small Roman letters will then be secondary individuals, belonging to the secondary series and arising from secondary masses, etc. It is to be observed that this indifferent tissue is here found only at the tips of branches or *Anlage* of such. No asterisks are found adjacent to the adult polypides A, B, C, etc., which have given rise to lateral branches, and these have therefore no power of producing new parts of the colony. The asterisks must not be regarded as having been descended from the letters which they adjoin, but from the terminal asterisks only; that is to say, in Paludicella embryonic tissue has originated from terminal embryonic tissue, and not from indifferent tissue left remaining alongside of the polypides.

Conditions differing in an interesting manner from these were found by Braem ('90, pp. 18–32) and myself (Davenport, '90, pp. 103–106) in Phylactolæmata. In *Plumatella* Braem has shown in the clearest manner how some of the embryonic tissue around a polypide at the proximal end of a nascent branch is carried away to the oral side of the "mother polypide," and lays the foundations of another polypide. In like manner the embryonic tissue around the "mother polypide" may give rise to one or several additional embryonic masses. He has also (pp. 29–32) shown in the most convincing way that each mass, particularly in the case of secondary buds, consists of two parts, of which one goes to form the polypide; the other contributes to the further growth of the common cystid and the formation of new embryonic masses. Since here every embryonic mass is in intimate relation with a polypide, and since the polypides arise nearly in one plane, only secondarily moving out from it, the relation of individuals may be expressed by a formula occupying a single line. Braem has thus expressed it: —

(2)



According to the system adopted for Paludicella, this may be given thus: —

(3) $*\alpha \quad *a \quad *b \quad *A \quad *a \quad *B \quad *C \ \ast$

or, more developed, thus: —

(4) $*\alpha_1 \quad *\alpha \quad *\beta \quad *a \quad *\alpha \quad *b \quad *c \quad *A \quad *\alpha \quad *a \quad *b \quad *B \quad *a * C \quad *D \ \ast$

in both of which the right hand asterisk (✱) takes the place of the A at the right of Braem's diagram. These symbols denote that we have a mass of indifferent tissue connected with each polypide, or the *Anlage* of such; and this indifferent mass, as well as the adjacent polypide, was derived from some other indifferent mass. Thus the masses connected with A, B, C, D are to be regarded as having been cut off from the embryonic mass at the extreme right; and each of these secondarily gives rise to the polypide buds a, b, etc., and their embryonic tissue. Thus we have to do with centrifugal budding only.

In *Cristatella* the conditions are essentially similar to those in Plumatella, the chief difference being that usually only two polypides with their embryonic masses arise from each polypide. This condition may be represented by the formula: —

(5) $*\alpha_1 \quad *a \quad *\beta \quad *a \quad *\alpha \quad *b \quad [*]A \quad *\alpha \quad *a \quad *b \quad [*]B \qquad [\ast]$

in which the embryonic masses originally attached to A, B, etc., are bracketed to indicate that they are normally no longer active in giving rise to new polypides. As a matter of fact, the secondary rows often make a greater or less angle with the primary ones, and as a result lateral branches are formed. Taking this character into account, the Cristatella formula might be written : —

$$\begin{tikzcd}[row sep=small, column sep=small]
 & & & & & & * \\
 & & & & & * & \mathrm{b} \arrow[d, dash] \\
 & & & *\alpha_1 \arrow[rr, dash] & & \alpha \arrow[d, dash] & {[*]} \\
 & & *\beta \arrow[rrr, dash] & & & *\mathrm{a} \arrow[r, dash] & \mathrm{A} \arrow[d, dash] \\
 *\mathrm{b} \arrow[rrrr, dash] & & & & {[*]}\mathrm{B} \arrow[d, dash] \arrow[rr, dash] & & {[*]} \\
 & *\alpha \arrow[rrr, dash] & & & \mathrm{a} & & \\
 & & & & * & &
\end{tikzcd} \qquad (6)$$

This representation indicates the fact that the first formed buds (A, a, *α*, etc.) are lateral ones; the second, median (Davenport, '90, p. 106). Intermediate stages between the condition in Plumatella, in which an indefinite number of polypides and gemmiparous masses can be budded off from pre-existing gemmiparous masses, and the condition in Cristatella, in which only two such arise, occur apparently in some species of Plumatella, in which, as Braem ('90, p. 31) has shown, few polypides are produced from any gemmiparous mass, and all but two of these generally do not develop. In the young corms of Cristatella, on the other hand, more than two polypides may thus arise.

Other *Ctenostomata* show a regularity in the budding process similar to that of Paludicella, and exhibit instructive variations upon it.

Victorella, an interesting Ctenostome occurring in slightly brackish water, and first described by Kent ('70) in 1870, possesses, according to the pregnant observations of Kraepelin ('87, pp. 75, 76, 154–157), a stolon-like tube, from which at intervals polypide-bearing "cylindrical cells" arise. Kraepelin ('87, pp. 155–159) has shown it to be in the highest degree probable that the protrusion of the body wall in the neck region of the polypide of Paludicella is the homologue of the "cylindrical cells" of Victorella, and that the remainder of the zooecia of Paludicella is homologous with the "stolon" of Victorella. While in Victorella the cylindrical cell is developed to such an extent that the retracted polypide is still included within it, and the stolon remains of small calibre, in Paludicella, owing to its shortening, the retracted polypide must seek refuge in the stolon, whose diameter is consequently increased to receive it. Evidence for this is found in the stolon-like nature of the youngest zooecia of a hatching winter bud of Paludicella Ehrenbergii, and in the elongated cylindrical cell of the adult Paludicella Mülleri, Kraepelin, in which the heavy asterisks represent the budding tips of the stock, which give rise to new individuals (tips of the stolons), and α_1, β_1, etc. indicate individuals of the fourth order. The lighter asterisks indicate, as before, points of proliferation from which new buds may arise.

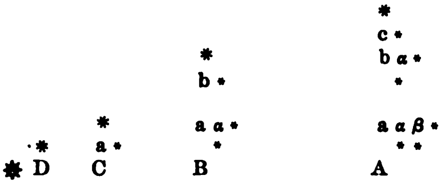
It seems highly probable that Victorella finds near allies in Mimosella and other genera of the Stolonifera.

In *Hypophorella expansa*, according to Ehlers ('76, pp. 5–9) and Joyeux-Laffuie ('88, pp. 137–139), the stolon is composed (as in Victorella), of a number of internodes, each separated from the other by communication plates, and bearing on the distal end typically a feeding zoöid (Nährthier) and a lateral stolon. It seems to me that the jointed condition of the stolon is reasonably accounted for in the same way as that of Victorella, by supposing that each internode, together with its zoœcium, is comparable with the whole indvidual of Paludicella. The "feeding zoöids" of Hypophorella will then be comparable with the *Cylinderzelle* of Victorella. Two facts are opposed to this view: first, the polypide is not formed primarily in the stolon, coming only secondarily to lie in the *Cylinderzelle* as in Victorella; and, secondly, there is a *Rosettenplatte* in Hypophorella between the feeding zoöid and the stolon, while none exists in Victorella. But upon this assumption one can best account for the fact that the stolon is composed of as many joints as there are feeding zoöids, — a condition which appears to occur in only a few other genera, and these closely allied to Victorella. Thus, in Cylindrœcium pusillum and C. dilatatum of Hincks we have two species which may be considered to represent two possible intermediate stages between Victorella and Hypophorella, not only on account of the jointed stolon, but also on account of the enlarged distal end of the joint, which is eminently characteristic of the allies of Victorella. The first objection, that the polypide is not developed in the stolon, but first arises in the well formed zoœcium of the feeding zoöid, might result from the increased importance of the zoœcium over the *Cylinderzelle*. The formation of the plate between the zoœcium and the stolon might be accounted for by the physiological need of such an organ resulting from the increased importance of the zoœcium (cf. p. 40). Such plates exist, in fact, between the primary median individuals, and those secondary median ones in Victorella which are budded from the *Cylinderzelle*. This hypothesis

far as they go, may not fit the conditions in all parts of the colony. Moreover, it is to a certain degree idealized, i. e. subjective, for even in the figure of Kraepelin ('87, Fig. 75) one of the individuals of the series a, b, c, etc. has given rise to no stolon as its first bud.

is further supported by the fact that, as a stolon may arise from the *Cylinderzelle* of Victorella, so in Hypophorella such a condition is not uncommon, although hardly typical. In accordance with this hypothesis the formula for Hypophorella might be given thus: —

(9)



Ehlers ('76, pp. 127, 128), in founding the group of Stolonifera, classified the different methods of arrangement of the individuals in the colony as follows: —

- I. Many polypides (*Nährthiere*) on the single joints of the stolon (*Stengelgliedern*).
  - 1. On the entire length of the joints.
    - (a.) Arranged in two rows.
    - (b.) Arranged in a spiral.
    - (c.) Arranged in one row.
  - 2. At the ends of the joints.
    - (a.) In rows.
    - (b.) Massed.
- II. Only one polypide *Nährthier* on a joint of the stolon.
  - 1. Polypide lateral, near it one or many stolonic joints (Hypophorella).
  - 2. Polypide terminal.

In the present state of our knowledge, it is very difficult to say how the types of budding shown in those Stolonifera which possess more than one *Nährthier* on a joint of the stolon are related to, or are to be connected with, the types of Paludicella, Victorella, Hypophorella, or other genera possessing only one *Nährthier* to a joint. This could doubtless be determined, however, by studying the early stages in the development of the stocks. Taking them as they are, however, we find a very simple condition in the stocks of Class I., in which the *Nährthiere* are arranged in a single row, as in *Vesicularia spinosa* (cf. Hincks, '80, Plate 73, Figs. 3–7). The tip of the stolon consists, as I have myself observed in allied species, of somewhat cubical cells of variable thickness, and it is from this tip that the *Anlagen* of the individuals arise. Lateral branches occasionally replace a *Nährthier*, and the latter seems never to produce secondary individuals. The formula of the stock might be written: —

$$(10)\qquad \begin{array}{ccccccccccccccc} & & & & & & & & & & & & \ast & & \\ & & & & & & & & & & & & b & & \\ & & & & & & & & & & & & a & & \\ \ast F & — & E & — & | & — & D & — & C & — & B & — & | & — & A \\ & & & & a & & & & & & & & & & \\ & & & & \ast & & & & & & & & & & \end{array}$$

In *Bowerbankia pustulosa* we have two rows of individuals produced side by side from near the end of the stolon. This condition would be represented by

$$(11)\qquad \begin{array}{ccccc} \ast & \ast D & \ast C & \ast B & \ast A \\ \ast & \ast D & \ast C & \ast B & \ast A \end{array}$$

provided the individuals of this primary series possess the power of giving rise occasionally to secondary buds, as seems certainly to be the case in some members of this genus which I have seen. The spiral arrangement of some colonies is striking; it is of evident advantage to the stock, but its cause in these cases is wholly unknown.

In every one of these cases, and, in fact, in all of those figured by Hincks, which belong to the Stolonifera, there is no trace of dichotomy. Throughout we have to do with linear series, which give rise to lateral branches.

Turning now from the Stolonifera to the other grand division of Ctenostomata, the *Alcyoniidæ*, we find the same prevalence of a law in budding. In its typical expression it may be written as follows: —

$$(12)\qquad \begin{array}{ccccccccc} & & & & & & \ast & & \\ & & & & & \ast & b & \ast & \\ & & \ast & & & \ast & (\ast) & \ast & \\ & \ast & a & \ast & \ast & a & a & a & \ast \\ \ast & & & & & \ast & & \ast & \\ \ast\ C & & (\ast)\ B & & & & (\ast)\ A & & \\ \ast & & & & & \ast & & \ast & \\ & \ast & a & \ast & \ast & a & a & a & \ast \\ & & \ast & & & \ast & (\ast) & \ast & \\ & & & & & \ast & b & \ast & \\ & & & & & & \ast & & \end{array}$$

Although secondary median individuals are not habitually formed, yet, owing to the capacity of regeneration possessed by individuals A, B, C, etc., an asterisk is affixed in parentheses to show the probable persistence of embryonic tissue. Of the lateral series one or both may fail to be developed.

It might be difficult to determine whether in this group we have to do with dichotomy, did not the tips of the margins at times reveal the fact that there is no division of the ancestral series, but that a new one is added at the side of an ancestral one (Plate VIII. Fig. 69), where of the marginal individuals 4 is clearly median (ancestral) and 3 is lateral, 13 median and 12 lateral, etc. (see page 49).

The members of the group of *Cyclostomata* seem to be closely related, and the method of budding is so similar throughout the group that it seems fair to interpret the more compact Tubuliporidæ from the Crisiadæ. In *Crisia*, as we have seen, individuals are placed in rows, from which at intervals lateral rows are given off to the right or left. One may say that typically these are given off from each individual to both the right and the left, although in some cases, as in Figure 65ᵃ, lateral branches are typically given off alternately to the right and left, and are often aborted. Perhaps the most general formula of all for Cyclostomes should be that of two lateral branches from each individual, one or both of which may remain undeveloped. Such a formula I believe to be also the typical one for *Bugula* and its allies, and for the *Flustrina* and *Escharina*. It would be written thus: —

```
                                                                    *
                                                                  * c *

                                                                *  (*)  *
                                                              * α   b   α *
                                           *                    *       *
                                         * b *
                                                            *   *  (*)  *   *
                         *              * (*) *          *  β * α   a   α * β  *
                      *  a  *        *  α  a  α  *          *   *       *   *
          *                             *     *
(13)   ✲  D          (*) C         (*) B                    (*) A
          *                             *     *
                      *  a  *         * α  a  α *           *   *       *   *
                         *              * (*) *         *  β (*) α  a  α (*) β  *
                                                            *   *  (*)  *   *
                                        *  b  *
                                           *                    *       *
                                                              * α   b   α *
                                                                *  (*)  *

                                                                *   c   *
                                                                    *
```

in which the parenthesized asterisks indicate the presence of regenerative tissue. This is identical with (12) and similar to (1).

Braem ('90, pp. 130–133) has already called attention to the difference between Phylactolæmata and Gymnolæmata in the *orientation of the* *polypide.* In Phylactolæmata the oral aspect of the polypide is turned towards the margin of the corm or the tip of the branching stock; in Gymnolæmata, on the contrary, the anal aspect is turned in that direction. This difference is a very striking and constant one. It is correlated with another difference in the law of budding of the stock, which will become evident upon comparing Formulas (4) and (5) on page 74, of Phylactolæmata, with Formulas (1) on page 73 and (7) to (13). In all of these the margin or tip of the stock is at the left, the centre at the right. In the formulæ of Phylactolæmata the budding is *centrifugal*, new individuals being produced from the embryonic masses towards the margin; in the formulæ of Gymnolæmata budding is *centripetal*, new individuals being produced from the embryonic masses towards the centre. *In both Phylactolæmata and Gymnolæmata the anal aspect is turned towards the gemmiferous region.*

Braem calls attention to one other difference, namely, that, in the case of the retracted polypide, in Paludicella the rectum lies next the attached surface of the stock; in Phylactolæmata, the œsophagus. A mechanical cause of this is suggested when this statement is put in other words: the polypide in its retracted position is stored in both Phylactolæmata and Gymnolæmata proximad of the atrial opening; i. e. away from the tip or margin, and towards the centre of the stock. May not this be explained, in part at least, as an adaptation to room?

I will here add four examples of regular budding taken from other groups of animals, to illustrate the general applicability of this method of representation. The first of these is that of the Siphonophore *Halistemma* whose formula has been worked out by Chun ('88, p. 1169), and expanded and illustrated by Korschelt und Heider in their recent textbook (p. 39). It runs as follows: —

(14) D c b a C d c b a B e d c b α a γ β α A

According to my interpretation of the case, this formula might be written (15): —

❋D ❋c *b *a *C ❋d *c *b *a *B ❋ *e *d *c *b *α *a *γ *β *α *A,

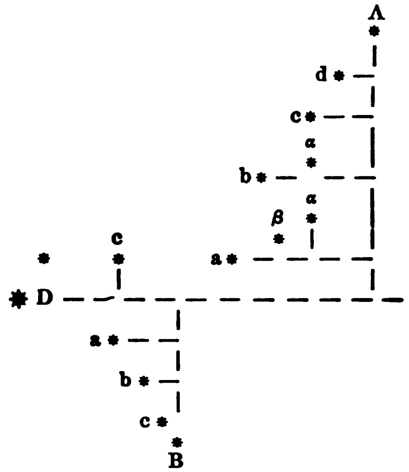
in which the ❋ behind B has been derived from the embryonic mass at A, that behind C from B., etc. The ❋'s represent embryonic masses from which a, b, c, etc. are derived.

If we assume that the terminal individual (A) has not been derived from the primary embryonic mass, at the extreme left, but has had its origin in the embryo, the formula would have to be written somewhat differently; namely, thus (16): —

✹ C✹ c* b* a* B✹ d* c* b* a* A✹ e* d* c* b* α* a* γ* β* α* [A]

In a species of *Pennaria*, common on our coast, which is probably Pennaria tiarella, McCready,[1] I have noticed the presence of a similar law of budding. The whole stock lies in one plane, the lateral branches arising alternately from the right and left of a central stock, like the barbs of a feather. These lateral branches give rise to a series of secondary ones, which are all placed on the same (axial) side of the branch. Each branch, of whatever degree, originates as a bud bearing a polyp. From the elongating stalk of this terminal polyp, buds arise, — the beginnings of branches of the next higher order. The stock may be represented by the following formula: —

(17)



Expressed in a linear series, this formula may be written: —

(18) ✹ D* C* B* c* b* a* A* d* c* b* α* a* β* α*

which is identical in form with the second formula (16) given for Halistemma.

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[1] This species is figured by Leidy ('55, Plate 10, Figs. 1-5) and Verrill ('73, Plate XXXVII. Fig. 277). An allied species, P. gibbosa, is figured by Louis Agassiz in the "Contributions" (Vol. III., Plate XV. Fig. 1). In describing P. Carolinii, Weismann (Entstehung der Sexualzellen, p. 122) says that the lateral hydranths do not possess the capacity of giving rise to new lateral hydranth-buds (of a higher order). But, as indicated above, P. tiarella seems to do this regularly. Leidy's and Verrill's figures show the same thing.

Lastly, this formula may be applied to certain cases of fission, as in *fresh water Annelids*. As is well known, the fissiparous process is preceded by the formation of the so-called budding zones (Knospungszone). These arise in *Ctenodrilus*, according to Kennel ('82, pp. 403, 404), between two dissepiments in the middle of a metamere, and new ones are continually formed behind the others as the animal grows in length by cell proliferation at the tail end. The budding zones are, according to Kennel, regions composed of embryonic cells. I think it probable that this embryonic tissue has been derived from the embryonic tissue of the anal end of the animal. There are as many budding zones produced as there are new metameres added by the anal growth, and since the budding zones are intrasegmental, each zoöid consists of four parts; viz. (naming them from anterior to posterior end) of the posterior half of the preceding budding zone, of the posterior half of the metamere in which the budding zone arose, of the anterior part of the next following metamere, and, finally, of the anterior part of the following budding zone. Zoöids then are made up of parts of two adjacent metameres, and the middle of each zoöid is intersegmental. The zoöid has progressed little beyond the state of possessing two (half) metameres at the time it becomes free. New metameres must become formed by caudal growth. The animal is, then, according to my conception of the significance of the process, derived chiefly from these budding zones. Evidently, the law of production of new individuals (or new budding zones) is a simple one, and may be written, in accordance with my nomenclature,

(19) ❊ E (*) * D (*) * C (*) * B (*) * A

in which A, B, C, etc. represent successive individuals (adjacent halves of two metameres), and the asterisks, as before, embryonic tissue. The two adjacent asterisks together represent the budding zone, of which the posterior half (parenthesized) proves itself the least active.

The conditions given by Semper ('77, pp. 69, 77) for *Chætogaster* (and Nais) are much more complicated, but may be expressed by the use of a formula constructed upon the same plan. Chætogaster differs from Ctenodrilus in this: that young budding zones, and eventually young individuals, are produced between older ones, instead of always at the anal end; and the new zoöids often acquire several metameres before becoming free. It seems to me probable that, as in Ctenodrilus, the budding zones are derived ultimately from the anal zone; but here, in contradistinction to Ctenodrilus, new budding zones may secondarily arise from other budding zones produced earlier, thus giving rise to the phenomena of young individuals interpolated between older ones. Representing, then, individuals by the budding zones from which they have arisen, we may convert the following formula of Semper into one based on our own nomenclature :

$$\mathit{az.} - \overbrace{3+0}^{\mathrm{E}} - 0 \quad \overbrace{4+0}^{\mathrm{D}} - \overbrace{1+0}^{\mathrm{H}} - 0 \quad \overbrace{4+1}^{\mathrm{B}} - \overbrace{1+0}^{\mathrm{G}} - 0 \quad \overbrace{4+0}^{\mathrm{C}} - \overbrace{2+0}^{\mathrm{F}} - 0 \quad \overbrace{4+1}^{\mathrm{A}}$$

in which the succession of generations of zoöids is

. . . 5, 4, 8, 2, 7, 3, 6, 1.

In the above formula A, B, C, etc. represent zoöids; the numerals below the letters, the number of metameres of which each is composed; 0, an incomplete metamere about to be derived from a budding zone; *az.*, the anal zone. Written in accordance with my conception of the facts, this formula would read :

(20) ❋ D (✱) ✱ C (✱) ✱ a (✱) ✱ B (✱) ✱ b (✱) ✱ a (✱) ✱ a′ (✱) ✱ A,

which somewhat resembles Formula (15) of Halistemma, and signifies that two embryonic masses are left behind by the anal zone, of which the one anterior to the zoöids proper (represented by letters) goes merely to form the head parts, and is represented parenthesized. The second is caudad the zoöid, and may form a secondary "anal zone" giving rise to new zoöids. From one zoöid two or more anal zones may take their origin. Thus, from the embryonic mass caudad of A there have arisen that caudad of b, which has given rise to b (✱) ✱ a (✱), and that caudad of a′, which has given rise to a′ (✱).[1]

The most general formula given on page 81 undergoes many modifications in the different groups, but in the midst of these modifications certain laws are to be discerned, to some of which I have already called attention. I will now proceed to a discussion of the significance of these laws.

The *quincunx* arrangement of individuals, which is so noticeable in the phytoid stocks of Bugula, and in creeping corms like Lepralia or Cristatella, may be explained as affording additional strength on the one hand, and as a device for saving space on the other.

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[1] From a study of surface views of many specimens of Autolytus collected at Newport during June, 1891, I am convinced that the sexual individuals are produced by proliferation of cells in the metamere XIII. or XIV. of "parent form," — the last which remains behind after breaking off of sexual form. Representing the proliferating metamere by (❋), we may write the budding formula of Autolytus thus:

(20^{a}) ❋ E (✱) D (✱) C (✱) B (✱) A (✱)

in which the parenthesized asterisks indicate the proliferating, but not gemmiferating anal metameres of the sexual form. (Cf. A. Agassiz, '63, pp. 397-400.)

The absence of true dichotomy, which I have sought to show characterizes the budding of Bryozoa, is interesting as seeming to indicate the fundamental similarity of the process of budding in Paludicella to that found elsewhere. The tip of the branch does not divide equally in the first nor in the other instances, but constantly maintains its precedence, giving off parts of itself to form lateral branches. These parts may grow out at right angles to the primary branch, as in Paludicella, but generally they grow forward nearly parallel to it, as in most marine Gymnolæmata.

In Bugula (Plate VII. Fig. 64^a) branches are always given off *toward the axils*, and therefore an ancestral branch gives off all lateral branches from one side and the successive orders of branches are given off alternately to the right and left. In Crisia, on the contrary, branches are given off *abaxially*, and they are given off not from one side only, but alternately to the right and left. In both cases the two facts are mutually dependent. The first case gives rise to a stock in which the branching tends as greatly as possible towards compactness and the formation of a closely built stock; the second case gives rise to a diffuse and loosely built stock (cf. Figs. 64, 65, and 64^a, 65^a). In the second case there is a maximum space to each individual; in the first, a maximum *economy* of space.

The rule that lateral buds on two closely related branches tend to arise in the same generation is one that, as has been shown, is more or less apparent in some cases, but is easily obscured by other rules. May not the tendency be due to the same causes that produce the synchronism of division in related cells of a cleaving egg?

That lateral buds should occur in *Bugula flabellata* on the outermost rows only is not surprising when we reflect that there is abundant room on the margin, whereas the inner individuals are hemmed in from lateral expansion by the pressure of adjacent rows. This is very marked in certain repent colonies, as, for instance, occasionally in Membranipora (Plate VIII. Fig. 70). Here the intermediate branches 6, 7, 8, and 9 have produced no lateral buds for many generations, while almost every individual of the marginal rows has given rise to a lateral branch. It is merely a result of the same cause, it seems to me, that lateral budding occurs more frequently in *Bugula turrita* at the margins of fans than elsewhere. Here there is room to spread.

The rule (5) that ancestral rows contain fewer *generations* of individuals than lateral ones may perhaps receive a partial explanation from the further fact (rule 6) that of the two rows starting from any axil the ancestral branch will give rise to a greater *total number* of individuals than the lateral one will in the same time. We should expect a less rapid forward growth if the lateral growth is extremely vigorous. One might also say that the intermediate rows had grown abnormally in length, since that is the direction in which there is most room.

The reason why the ancestral branches in Bugula give rise to the greater total number of individuals is, to my mind, because they are marginal. In Crisia it is the lateral branches which are the most prolific, and for the same reason.

The existence of the 7th rule in mat-like species is a mechanical necessity; in the phytoid species, like Bugula and Crisia, it must be accounted for on another ground; namely, on the relations of food supply to demand, — on the deterrent effects of overcrowding. And this, to my mind, is the key to the significance of the 4th, 5th, 6th, and 7th rules. The form of the stock is determined by the same law which has determined the form of the individuals, — the struggle for existence and the survival of the fittest, — the fittest in the present case being those which are most advantageously placed with reference to food supply. Abundant food supply has made possible the rapid production of lateral individuals at the margin, and less abundant food supply has retarded such production in the middle. Therefore has lateral budding occurred more rapidly at the margin; therefore has the number of individuals produced at the margin been greatest; therefore have the median rows grown *in length only* with great rapidity; therefore has the distance between adjacent rows of individuals in phytoid stocks remained constant.

Many observations on different groups of animals agree in demonstrating a relation between rapidity of the budding or fission process and food supply. Thus Zoja ('90, pp. 25–27) has shown for Hydra, and Zacharias ('86, p. 274) and von Wagner ('90, p. 360) for Turbellarians, that abundant food supply results in an acceleration of the processes of non-sexual reproduction, and Braem ('90, p. 24) has shown that budding in Cristatella proceeds less actively during the late fall. This diminution in activity has been attributed by Braem to diminished temperature; but we know also that this period is one of scarcity of the small fresh water organisms upon which the fresh water Bryozoa live (cf. Parker, '90, pp. 597–600), and this fact also must be considered as having an important influence in this case.

II. Relation of the Observations on Budding in Bryozoa to the Germ Layer Theory.

No question in Bryozoan morphology has been more thoroughly discussed than that of the part played by the germ layers in the production of the polypide, and upon none has there been less agreement. Nitsche first boldly opened the question, and concluded that we have in this process a fatal objection to the idea of the homology of the germ layers, in so far as their homology depends upon a similarity of fate throughout the Metazoa. A single layer, the invaginated ectoderm, gives rise to the outer covering of the tentacles, to the pharynx, and to the brain, — structures elsewhere considered as ectodermal, — and also to the lining of the alimentary tract, elsewhere universally accounted entodermal. In view of these facts, "sind die Keimblätter," concludes Nitsche ('75, p. 398), "keineswegs mit einer besonderen histologischen Prädisposition ausgestattete Zellschichten, sondern lediglich die flächenhaft ausgebreiteten Elemente, aus denen die den Metazoenkörper zusammensetzenden, ineinander geschachtelten Röhren sich bilden." Prouho, although recognizing the facts to be as stated by Nitsche, has not discussed the theoretical bearing of the question. Seeliger ('89^a, p. 204) finds in the budding process of Endoprocta a shortening and confusion of the embryonic process. "Wie die gesammte Knospenentwicklung verkürzt ist, erscheinen auch die beiden Processe der Einstülpung durch welche im Embryo zuerst Entodermkanal, dann Atrium sich bilden, in einen zusammengezogen." In another place (Seeliger, '90, p. 595) the budding process is considered as an "immer sich erneuerende Gastrulationsvorgang." Braem ('90, p. 116) regards the inner layer of the bud as entoderm, and the process of its formation as one of gastrulation. In a preliminary notice published last February (Davenport, '91, p. 279) I suggested that the embryonic tissue from which the inner layer of the polypide arises is to be regarded as "neither ectoderm nor entoderm, but as still indifferent, and capable of giving rise to either." A few weeks ago I saw for the first time the paper of Oka ('90), in which he offers (p. 145) *a priori* a similar suggestion concerning the significance of the embryonic tissue from which the inner layer of the polypides arises. I am pleased to find that our ideas, thus independently arrived at, are so fully in agreement. My idea of the relation of the germ layers to the layers of the polypide bud chiefly grew out of my studies on the embryology of Phylactolæmata as described in earlier pages.

As there are two layers to the bud, the question of the part taken by the germ layers in the polypide bud may be subdivided into two: What is the significance of the outer layer of the bud? and, What is the significance of the inner?

The *outer layer of the bud* is derived from the cœlomic epithelium. The views of those who have studied the formation of this inner layer of the cystid in Phylactolæmata may be classed in two categories: (1) those in which it is regarded as entoderm, and the process of its formation as gastrulation; and (2) those in which it is regarded as mesoderm. To the former class belong the views of Reinhard ('80, p. 208), Korotneff ('89, p. 403), and Jullien ('90, p. 19); to the latter, those of Kraepelin ('86, p. 601) and Braem ('90, p. 116), and in this class the views of Barrois ('86, p. 68) and Haddon ('83, p. 543), founded on *a priori* considerations, must be placed.

It seems to me that, since, as Barrois has demonstrated, there is a great similarity between the Phylactolæmatous and Gymnolæmatous larvæ, and especially since the former show evident signs of degeneration, we are bound to study the phenomena they exhibit in the light of our knowledge of the ontogeny of Gymnolæmata.

But first it is necessary to give reasons for believing that the larva of Phylactolæmata is to be regarded as homologous with that of Gymnolæmata; and to do this I will first name the points of similarity in the two larvæ, and then try to show that the differences which exist are not sufficient to invalidate the attempt to establish a homology. And, first of all, it may be said that, since the adult Phylactolæmata and Gymnolæmata are strikingly similar to each other, and since no one doubts their close relationship, we should expect *a priori* that their larvæ would be homologous, especially since the larvæ of Gymnolæmata are admitted to belong to the trochosphere type, of whose ancient origin there can be little doubt. In the second place, the very existence of a larval stage in Phylactolæmata is indicative of its inheritance from an earlier condition, for two reasons: (*a*) because in general fresh-water life tends to eliminate larval stages from species which have inherited them from marine ancestors, and tends little to form them *de novo* (Hydra, fresh-water Turbellarians, Rotifera, Oligochæta, Hirudinea, Astacus, and fresh-water Mollusca); and (*b*) because, specifically, the early stages of development of Phylactolæmata are passed within a uterus-like sac, from which the embryo is released only when a colony is already well established. In the third place, the Phylactolæmatous larva possesses, in common with all Gymnolæmatous larvæ, the following characteristics. The primary polypides arise in both at a pole, and this pole is in both a prominent disk, surrounded by a circular fold, — the so-called mantle fold, — from which it is separated by a circular groove, — the so-called mantle cavity. This organ has a similar origin and fate in the two groups, as shown by Barrois.

The following points of difference, however, must be recognized. First, the absence of a definite ciliated ring, *couronne* (Barrois), of an internal sac, and of a pyriform organ. But, as Barrois ('86, p. 67) has shown, these are absent, or at least (Ostroumoff, '87, pp. 182, 183) little developed, in Cyclostomatous Bryozoa. The ciliated ring and pyriform organ are doubtless organs connected with a free locomotive larval life, which is greatly abbreviated in Phylactolæmata. A second difference exists in the fact that, while most Gymnolæmatous larvæ possess either, rarely, (1) a functional alimentary tract, or (2) a mass of loose tissue lying inside of the ectoderm, the Phylactolæmata possess (3) a central space lined by an epithelium placed next to the ectoderm. However great the difference between the first and third conditions mentioned above, it is to a large extent bridged over by the widespread existence of the second. In some Cyclostomes, moreover, a similar condition to that in Phylactolæmata seems to exist. Compare Metschnikoff ('82, p. 310, Taf. XX. Fig. 62). Lastly, the origin of two primary polypides, instead of one, at the aboral pole, upon which Barrois has laid some stress, cannot be considered a very strong objection to the homology, because in reality the two polypides do not arise at the same time even in Plumatella, and in Cristatella this difference is still more pronounced. In fact, it is not the formation of *two polypides* which requires explanation, but that of a young *stock* before hatching.

There remains, therefore, to my mind, no serious objection to regarding the larvæ of Phylactolæmata and Gymnolæmata as having been derived from some common ancestral larva, possessing, of course, more points of resemblance to the Gymnolæmatous than to the Phylactolæmatous type; and therefore it is perfectly justifiable to interpret the latter by aid of the former.

Admitting the larvæ to be homologous, we should expect the process of *gastrulation* to be comparable throughout Ectoprocta. As a matter of fact, we do find a great similarity in the earliest stages. Thus, the first indication of the inner layer is the ingression of four cells at one pole, which by multiplication give rise to a layer of cells lying inside of the ectoderm.[1] It is to the comparative study of the fate of this inner layer in the different Ectoproct larvæ that we must look for an explanation of the layer in the specific case of the Phylactolæmata.

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[1] This has been shown for Membranipora (Tendra) by Repiachoff ('78, pp. 416–420); for Alcyonidium polyoum by Harmer ('87, pp. 445, 446); for Bugula by Vigelius ('86, p. 519); and for Cristatella in the present paper (page 68).

For the purposes of this study, it is desirable to begin with species in which there has been a minimum amount of degeneration. Such are Membranipora (Cyphonautes), Alcyonidium, and Flustrella, to which we must now turn our attention.

The studies of Repiachoff on Membranipora lead up to a stage in which the entoderm lies as a solid mass inside the ectoderm, and is separated from it at all points. Neither the origin of the mesoderm nor the formation of stomodæum or proctodæum was observed at this time. As for the fully formed Cyphonautes, it is certain, as I can confirm from personal observation, that there is a well developed functional alimentary tract, and that it is provided with a well developed muscular system, including cross-striped muscle fibres. There is, therefore, every reason for believing that typical entoderm and mesoderm have been formed in it.

In Alcyonidium (polyoum), Harmer ('87, p. 445) has shown that after gastrulation a great mass of cells occupies the former blastocœl. This, in the author's opinion, represents entoderm and mesoderm. The young larva possesses a mouth, an œsophagus, and a large stomach, but never an anus. No evidence is presented that the oral pole corresponds with the pole of ingression.

Flustrella, which is nearly related to the last species, possesses in its young larval stages a pocket, which Prouho ('90, pp. 424–426) has shown to represent the anterior part of the alimentary tract, directly comparable with that of Alcyonidium polyoum, but less developed. Muscle fibres and an epithelial lining of the entoderm and ectoderm exist to indicate the presence of mesodermal tissue.

These three genera, Membranipora, Alcyonidium, and Flustrella, are the only Ectoprocta in whose larvæ the presence of an alimentary tract has as yet been demonstrated.

In Bugula, a very careful study of which was made by Vigelius ('86 and '88), one finds after gastrulation and cell multiplication a mass of cells filling the whole interior of the larval body, at first appearing as an epithelium surrounding a central space, but later without arrangement and often showing signs of degenerescence. No definite separate mesoderm could be found, and at no time was any trace of an alimentary tract to be seen. Vigelius calls the mass derived from the four entodermal cells *Füllgewebe*, and he believes it to correspond morphologically to both "hypoblast and mesoblast." It is to be noted, however, as a point of considerable importance, that in his figures of the metamorphosing larva Vigelius ('88, Taf. XIX. Fig. 6) represents this tissue as having almost entirely disappeared; that which remains giving rise to the mesodermal lining — the outer layer of the bud — of the developing polypide.

There can be no doubt that the so-called oral pole of the Bugula larva corresponds to the mouth-bearing pole of Alcyonidium, but does it correspond to the pole of ingression of entoderm? This question has not been answered by Vigelius. The existence of homopolar stages like that represented in his ('86) Figure 25, Taf. XXVI., makes it very difficult to establish this doubtful point.

The formation of the inner layer of Cyclostomes has been studied by Barrois ('82, p. 141). He says: "Dès les premiers stades les sphères vitellines glissent les unes sur les autres de manière à former une espèce de gastrula par épibolie et l'on ne tarde pas à rencontrer des stades d'un volume extrêmement exigu et déjà composés d'une couche exodermique et d'une masse endodermique libre dans son intérieur. La masse endodermique s'atrophie rapidement et l'on arrive à une petite blastula qui succède non pas à un stade composé de cellules radiaires dans lequel se forme une cavité centrale, mais qui est issu, au contraire, d'une vraie gastrula née par épibolie dans les premiers stades de la segmentation et dans laquelle la masse endodermique est déjà disparue." I have quoted Barrois thus at length, since his description will show forcibly at least one thing, that the fate of the cells which by ingression had entered the blastocœl is quite different from that of those in Bugula, where a great *Füllgewebe* is formed. Ostroumoff ('87, p. 183), however, has shown that the inner layer of the Cyclostome larva does not disappear, but comes to line the ectoderm as a very thin layer. In the adult larva, however, we find the contents of the ectodermal sac "filled with mesenchymatous cells, which are commingled with yolk granules and globules of albumen." It is these cells that produce the very considerable mesodermal layer of the first polypide, which arises in the metamorphosis of the larva. Here, as elsewhere, an apparently homopolar stage intervenes between gastrulation and the formation of larval organs, making orientation difficult.

Thus, passing from Cyphonautes, through Alcyonidium and Flustrella, Bugula, and finally Cyclostomes, we have a series in all of which the inner germ layer is derived from one pole by ingression or by 'epiboly," and in which there is a gradual reduction of the functional entoderm until it seems, in Cyclostomes, to be lost, and a gradual transformation of the mesoderm from a cell mass nearly filling the larva, and producing muscles and a lining to the body wall and alimentary tract, to a single thin cell layer lying next to the ectoderm, or to mesenchymatous cells extending through the cœlom.

This same series may be said, also, to be one in which there is a gradual decline in the complexity of larval organs. These find their maximum development in the bivalve Cyphonautes and Flustrella, and the complicated and beautiful Alcyonidium larva. They find their minimum development in the Cyclostomes, whose larvæ, instead of a girdle of flagella, possess merely an undifferentiated clothing of cilia, are reduced to a cylindrical or ellipsoidal form, lack the pyriform organ of other species, and in some cases possess only the rudiment of the internal sac.

If we were to imagine still another term at the degraded end of the series, it would be a form in which the four inner-layer cells that arise by ingression at one pole of the larva should give rise to little or absolutely no entoderm, in which the mesoderm should come to form an inner lining to the ectoderm, and in which the internal sac should be entirely absent. It is just these conditions which are fulfilled by the Phylactolæmatous larva.

Of all these changes, the loss of the entoderm is the most striking. What can be said in explanation of it? I would suggest this hypothesis: that *the entoderm of the Bryozoan larva has become rudimentary through loss of the alimentary function.*

In direct support of this hypothesis I have little experimental evidence to offer. One observation, however, which I made last summer, seems to favor this conclusion strongly. This is that larval life is of considerable duration in Cyphonautes, which possesses a functional alimentary tract, but is very brief in Bugula, in which no alimentary tract arises. As is well known, Cyphonautes occurs in enormous numbers in the "tow" at certain seasons of the year, and this is alone evidence of a considerable length of life. I have taken Cyphonautes thus obtained from the tow and have kept them for three or four days, at the end of which time they died, or had settled to the bottom of the glass vessel to undergo their metamorphosis. In fact, from several hundred Cyphonautes which I collected, not more than half a dozen completed their full metamorphosis, the others apparently succumbing to unfavorable conditions.[1]

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[1] Just as the manuscript of this paper is going to the printer, after long delay caused by an accident necessitating the re-engraving of the plates, I find that Dr. Prouho read last summer ('90), before the Association Française pour l'Avancement de la Science, a preliminary communication on the development of Cyphonautes. This is published in the printed report of the proceedings of that association. The

The *Bugula* larvæ, on the contrary, I have never found in the tow, but they swarm out from stocks gathered in the morning and placed in a glass vessel; and I can confirm Nitsche's ('69, p. 9) observation that they settle and begin their metamorphosis within "a few hours" after hatching. One rarely or never finds these larvæ succumbing to the unfavorable conditions of the aquarium before metamorphosing. From these observations I conclude that the Bugula larva has a very much shorter life than Cyphonautes. Now, since the larva, owing to its shortened life, has no need of functional entoderm, and since entoderm can be of use to the larva only, no part of it going over into the tissues of the primary polypide of the stock (except as food material), functional entoderm is not developed. In other genera, its rudiments have become less and less important in the ontogeny, and, finally, in Phylactolæmata are wholly lost.

That the entoderm should reach its last stage of degeneration in *Phylactolæmata* is easily understood when we consider that the larval period is passed in a closed oœcium, from the wall or neck of which it receives nourishment *as a parasite does.* Moreover, by the delay in the period of hatching, as well as by precocious development of polypides, one at least of the latter is usually functional in the just hatched stock, for there is sometimes found at least one polypide in the newly hatched larva, which is partly extruded, and therefore capable of feeding, and thus of supplying the whole stock with nutriment. Of what advantage to a species could be the development of a functional larval entoderm, which should go to form no part of its adult tissue, provided the larva was contained in a uterus during its early stages, and was provided with the adult digestive organs in a functional condition before leaving the uterus?

Those who maintain that the inner layer is to be regarded as entoderm, and are still unwilling to place the Bryozoa among the Cœlenterata, must account for the absence of mesoderm. Korotneff ('89, p. 400) finds degenerating cells in the blastocœl before this is wholly obliterated by the extension of the inner layer. These he seems to regard as degenerate mesoderm. According to his view, then, the entoderm gives rise to the muscularis, — for this arises from the inner larval layer, according

author does not there state whether stomodæum and proctodæum are formed on the blastoporic side of the larva. He accounts for the existence of an alimentary tract in Cyphonautes by the fact that it undergoes its development disconnected with the parent, while almost all other Bryozoa pass their early stages in the parent or some protecting zoöid (oœcium, ovisac, ovicell).

to Braem's ('90, Taf. VII. Fig. 89 *mb.*) observations, which I can abundantly confirm, — and to the cœlomic epithelium of the adult stock. In the few series of sections of the proper stage which I possess, I have not found with certainty the degenerating cells of which Korotneff speaks; but even if they regularly occur, I should be inclined to regard them as the degenerated entoderm, the mesoderm persisting to give rise to the muscular tissue and the cœlomic epithelium.

From a consideration of these facts, — that the larvæ are homologous and the process of gastrulation is comparable throughout the Ectoprocta, that in the least modified larvæ both functional entoderm and mesoderm are produced by that gastrulation, that one of these two germ layers has become rudimentary in Phylactolæmata, that it is highly probable that the entoderm has disappeared from loss of function, and that the layer which persists gives rise to the musculature, sexual cells, and cœlomic epithelium, — I conclude that *the inner layer of the Phylactolæmatous larva, and therefore the outer layer of the bud, is mesoderm.*

If we accept the point of view of Kleinenberg ('86, pp. 1–19) and admit the existence in general of only two layers, ectoderm and entoderm, a clearer conception of the modification undergone by the Phylactolæmatous larva may be gained. We may divide the entoderm arising in Bryozoa into two parts; viz. (1) that which gives rise to the lining of the midgut, as in Cyphonautes, and (2) all the rest of the inner layer. Now, since no midgut is formed in the Phylactolæmatous larva, part (1) of the entoderm has ceased to be differentiated; all which remains, then, is part (2); but this is equivalent to "mesoderm" in the sense in which I have employed it, and therefore I am justified in saying that "mesoderm" only is produced.

The question has now to be answered, What is the significance of the *inner layer of the bud?* Two different answers have been given to this question. It has been maintained, on the one hand, that it is to be regarded as ectoderm; on the other, as entoderm. There are serious difficulties in the way of accepting the first view, — so serious, in fact, that few authors have maintained it, although at first glance it seems to be required by the facts. Although we have not yet sufficient grounds for declaring that organs formed by budding must be built up from the same germ layers as corresponding larval ones, — although we may admit that gemmigenesis recapitulates phylogeny and corresponds with ontogeny only in an imperfect and confused way, — still, from the experience gained by tracing the development of hundreds of animals from the most widely separated groups of the animal kingdom, the idea that a functional alimentary tract is ever wholly derived from differentiated ectoderm will not be accepted by most embryologists without conclusive evidence.

The second view is that the formation of the inner layer of the bud is a process of gastrulation, giving rise to entoderm, and that the so-called "gastrulation" of the sexual ontogeny of Phylactolæmata is to be regarded as a precocious ingression of mesoderm only.

Two considerations are opposed to this view. In Membranipora there is a gastrulation which gives rise to the entoderm and mesoderm of the larva; and since the gastrulation of Phylactolæmata is similar, these elements must be potentially present here also. The "gastrulation" in Bryozoa is a normal one; if there is any entoderm in the body wall giving rise to the inner layer of the bud, it must have been entoderm which failed to become invaginated. But what, in the second place, is to be gained by assuming that the inner layer of the bud is formed from entoderm? Here is as great a difficulty as before, since the nervous system originates from this layer. It has been maintained in many cases that the nervous system arises from *mesoderm*, and Seeliger ('89, p. 602) believes that it is formed from that layer in the non-sexual reproduction of some Tunicates; but I know of no good evidence of its origin in any of the Triploblastica from *entoderm*.

Before going on to state my conception of the significance of the inner polypide layer, I desire to call attention to the conditions in the region at which it is first formed. I have shown above (page 69) that the primary polypide or polypides arise from the pole of ingression in Phylactolæmata, and that therefore in this group the aboral pole (in the sense of Barrois) corresponds to the pole of ingression. As I understand Barrois, he means by oral pole merely the pole which in Cyphonautes, for instance, bears the mouth, — the pole also by which the larva attaches itself. Braem ('90, p. 123, foot-note), however, interprets "oral side" in Barrois's sense to mean in the last instance the place at which gastrulation takes place. Perhaps Barrois does somewhere state such to be the significance of his term (I have not found the place), but in that case I can only say that, to my mind, he has not produced sufficient evidence to prove that the oral pole of the larva of Gymnolæmata is the same as the pole of ingression in the gastrula; nor, in my opinion, has any other investigator done so. Nearly all species studied have a stage early in their development when their poles are very similar, and orientation certainly would be exceedingly difficult. One of the best figured series in which to trace the homology of poles is that shown by Repiachoff ('80, Taf III.) for Bowerbankia. So far as the figures go, one would conclude that Figure 10 A and its predecessors were oriented in the opposite direction to Figure 11 and its successors, which would result in placing the pole of ingression (Fig. 9) at the aboral pole of the larva, — the pole which here, as in all other Gymnolæmata, and, I believe, in Phylactolæmata also, gives rise to the primary polypide. I have given above additional evidence for this conclusion, in my argument to prove the homology of the larvæ and larval organs in Phylactolæmata and Gymnolæmata.

The polypides arise in Phylactolœmata at the pole of ingression, which is probably homologous with the aboral pole of Gymnolœmata. The pole of ingression, or the region of the lips of the blastopore, must be regarded as being a region of less pronounced differentiation than the rest of the gastrula. Its cells cannot be said to be either ectodermal or entodermal. It is an interesting fact, that it is just these indifferent cells — not yet either ectoderm or entoderm — that give rise to the inner layer of the polypide, from which organs usually considered ectodermal as well as those considered entodermal arise.

My conclusion, then, the objections to which I fully realize, may be stated in the following words: *The inner layer of the polypide bud is composed of cells derived from the rim of the blastopore. Such cells are to be regarded as still indifferent, and as first becoming differentiated into ectoderm and entoderm in the formation of the young polypide.*

Just when and where, on this hypothesis, the differentiation into ectoderm and entoderm occurs, is an important question; but unfortunately I cannot answer it decisively. It may be pointed out, however, that it has now been shown for most Ectoprocta that the lining of the middle part of the alimentary tract is formed independently of the œsophagus, and by an actual or potential outpocketing of the primitive simple sac of the bud. In Endoprocta there is a similar outpocketing, which, however, arises in connection with the œsophagus, and is formed independently of the rectum.

This is perhaps the proper place to call attention to the fact that the mesodermal outer layer of the bud has a very embryonic character at the budding region. This is indicated by the fact, that in Phylactolæmata (in which group alone I have studied the subject) eggs always arise from that part of the cœlomic epithelium which lies in the budding region (cf. Plate XI. Fig. 93). In Pyrosoma, also, according to the researches of Seeliger ('89, pp. 598–602) the mesoderm of the budding region, the stolon, gives rise to eggs. The same condition seems to exist in other Tunicates.

III. On some Characteristics of Gemmiparous Tissue.

In the preceding part of this paper the words "embryonic tissue," "undifferentiated tissue," have often recurred, and they are terms in wide usage in modern zoölogy. I do not know of any attempt to define further the real character of this tissue, nor to give its more detailed characteristics, other than that usually employed in the term *plasmareich*, or "rich in plasma." The persistence of yolk granules is, as Nussbaum ('80, pp. 2–14) and Goette ('75, pp. 31, 32, 831) have shown in the case of amphibian embryos, indicative of the *embryonic* condition of cells, when these have been derived from an egg filled with yolk.

It is very far from my purpose to go into a detailed discussion of the significance of embryonic tissue, for which I am not yet fitted; nevertheless, I wish to call attention to the minuter characters of gemmiparous tissue as I have found it in Phylactolæmata and Paludicella. I have described it in some detail in preceding pages.

First, then, gemmiparous tissue seems to stain more deeply than non-gemmiparous tissue in the same section. This character has been repeatedly observed before by others, and Braem calls attention to it several times. I have already described how I found, by the use of high powers, that much of this depth of stain was due to the unusually large number of deeply staining granules scattered through the cell, but chiefly gathered about the nucleus (Figs. 6, 17, 18, etc.). So marked is the greater depth of the stain around the nuclei, that, with a power so low that the nuclei are hardly distinguishable, their position is indicated by a deeply staining band.

Secondly, gemmiparous tissue, as I have found it in the cases referred to, is distinguished by the possession of large cells, nuclei, and nucleoli. I had already noticed this fact in my studies on budding in Cristatella, and I find that Braem has figured the nuclei in the budding region as larger than the average (cf. Braem, '90, Taf. VII. Figs. 86, 88–90). My own figures show this repeatedly (Plate I. Figs. 3, 4, 5, 6, Plate II. Figs. 15, 17, Plate XI. Fig. 99, etc.). I have also noticed this to a certain extent in the marine Bryozoa, but, since the cells of the latter are smaller, and as I did not succeed in obtaining from them sections so satisfactorily stained, the results are not so reliable. In attempting to obtain an explanation of this phenomenon one involuntarily recalls to mind the condition in young egg cells, where the nucleus attains a relatively enormous size. This great size of the nucleus in young egg cells is explained by Korschelt ('89, p. 92) as due to its participation in the trophic activity of the cell: "Sein grösster Umfang fällt in die Zeit des energischen Wachsthums der Eizelle." So in the gemmiparous regions the large size of the nuclei must be considered as connected with the growth of the cells.

But if the growth of the cells is accompanied by a rapid ingestion of food material (which the larger nucleus implies), some evidence of that fact should be observed in the cells themselves in the presence of food granules. Such food material in rapidly growing ovarian egg cells lies near the nucleus. Stuhlmann ('87, pp. 13, 14) describes such a condition in the ovary of Zoarces. "Neben dem Keimbläschen, jedoch ein klein wenig von seiner Membran entfernt, bilden sich an verschiedenen Stellen jetzt eigentümliche Verdichtungen des Protoplasmas, die sich ein wenig stärker mit Saffranin färben als das Zellplasma." Such a thickening of the protoplasma is represented in the figures as minute granules. Korschelt ('89, pp. 123–125) mentions several other such instances.

It has seemed to me possible to interpret the stainable granules lying near to the nucleus in gemmiparous tissue as such food material,[1] particularly since we know that food material does exist in the cœlomic epithelium lying next to the cells which are about to divide rapidly and to give rise to the inner layer of the polypide. That food is being taken in by the inner layer cells from the cœlomic epithelium is indicated by the fact that the nuclei of the former cells lie near the latter epithelium (cf. Figs. 15, 17, 18, 28, 56, etc.); for, as Korschelt has shown, the nucleus tends to move towards the centre of activity of the cell. That these granules observed in the cells are food material is indicated by their abundance in cells lying next to the reticulated cells of the cœlomic epithelium (Figs. 6, 28, 56).

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[1] Granules similar to these appear to exist in the protoplasm of all cells. It is their extraordinary abundance in the gemmiparous tissue upon which I lay stress. They have been variously interpreted by different authors. Bütschli ('88, pp. 1469–1472) describes various kinds of stainable granules in Ciliata which are food products, and the general character of which accords with that of the granules referred to above. "Excretion granules" of Ciliata do not stain, according to this author, which is an indication that the bodies in gemmiparous tissue are not such. I am particularly struck by the fact that the food products of Protozoa are chiefly found in parasitic forms, — Gregarinidæ and parasitic Ciliata. These take up food in solution from their hosts exactly as the cells of the body wall of Bryozoa do from the body cavity. Altmann ('90) has recently interpreted similar deeply staining granules in other cells, as "die Elementarorganismen." I can see no reason, on Altmann's theory, for the peculiar distribution of the granules that I have found.

My conclusion, then, is this: *Gemmiparous tissue is a rapidly assimilating tissue, possessing large nuclei because actively assimilating, and staining deeply because full of food material.*[1]

While for Nussbaum, as already quoted (page 71), "indifferent cells" are essential to the reproduction of individuals by non-sexual as well as by sexual methods, Seeliger ('90, p. 596) has concluded that "die Vorgänge bei der Knospung der Bryozoen uns zeigen, wie histologisch sehr bestimmt differenzirte Gewebe einen ganz embryonalen Charakter wiedergewinnen können. Mehr noch als bei der normalen Knospung am freien Stockende ist dieses Vermögen bei der Regeneration der Polypide der Ektoprokten oder der Köpfchen der Pedicellinen ausgebildet. In diesen Fällen sehen wir ein plasmaarmes, äusserest feines Plattenepithel, das über sich eine mächtige Cuticula ausgeschieden hat, sich in kubische und cylindrische plasmareiche Zellen zurückverwandeln und durch eine Einstülpung ein neues Polypid bilden, in welchem schliesslich die mannigfachsten Gewebsformen vertreten sind."

It seems to me that many facts in the budding of Bryozoa are strongly in favor of Nussbaum's hypothesis. On this assumption, we can best understand why in Cristatella there is not an invagination of the ectoderm, and why instead a stolon is formed in the embryo, which passes along at the base of the ectoderm and at intervals gives rise to the inner layer of the body wall. I believe it is because the outer layer of the body becomes so rapidly differentiated by the secretion of the gelatinous balls in its cells as to be incapacitated for the work of building organs. In Plumatella the outer layer of the body wall, which is derived, as Braem has shown, from the neck of the older polypide, retains for a long time its embryonic condition, so that its deeper cells can and do go to form the inner layer of the polypide bud.

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[1] Other observers describe gemmiparous tissue as being either rich in food or deeply staining. Seeliger ('85, p. 588) speaks thus of the mesodermal gemmiparous tissue in Salpa: "Die einzelnen Zellen sind grossblasig, enthalten einen runden Kern und führen Oel- und Fettsubstanzen die als Reservematerial beim Aufbau des embryonalen Leibes weiterhin in Verwendung gelangen." Von Wagner ('90, p. 377) says of the indifferent cells which are being transformed into the new pharynx of dividing Microstoma: "Dieselben nehmen an Grösse zu, . . . indem gleichzeitig ihre Protoplasmaleiber feinkörnig granulirt und für Farbstoffe imbibitionsfähiger werden."

In some sections of gemmules of Esperella fibrexilis, H. V. Wilson, of which Dr. Wilson has very kindly sent me several slides, I find the outer layer of young gemmules, in which the inner layer has been newly formed, stained very deeply. Observed with a Zeiss Apochr. 4.0 mm., Ocs. 8 and 12, the cell contents are seen to be evidently of two kinds, — light and deeply stained. The latter appearance is due, in part at least, to small dark granules, which can be discerned without much difficulty.

On Nussbaum's hypothesis we can best understand why in Paludicella the *Anlagen* of the lateral branches exist from the beginning as cuboidal cells, quite different from those of the rest of the body wall; we can understand why the cell layers of the margins of the stock, the tips of branches, and the ends of stolons from which buds arise, are thicker and more rapidly dividing than the rest of the body wall (cf. Figs. 14, 71, 73, 75); and we can also understand why the regenerating buds always arise from the region of the neck of the degenerated polypide, — the same region from which that degenerate polypide had arisen by budding.

There is no doubt, however, that at times buds do arise from tissue which, as Seeliger says, has lost its cuboidal nature only to regain it. From such tissue apparently the polypide of Figure 79 has arisen; from such tissue certainly, as Seeliger says, do regenerating polypides arise. But is the process by which cuboidal cells become a pavement epithelium one of so fundamental differentiation that, in accordance with Nussbaum's doctrine, we should not expect, under favorable conditions, to see these cells regain their cuboidal form? No doubt we have many other cases in the animal kingdom in which flat epithelial cells regain their cuboidal form. Thus, for instance, among the Bryozoa, Oka ('90, p. 132) has shown how the flat cells of the outer layer of the statoblast begin to thicken again at the return of warmth, and at the beginning of the active assimilative processes, not only at the pole from which the primary polypide is to arise, but also opposite to this.

Many facts indicate that cells may become flattened epithelia, and yet not lose their embryonic character. Maas ('90, pp. 541–544) has recently shown step by step how the columnar ectoderm of the fresh water sponge is forced, on account of the great increase in surface which it is called upon quickly to cover, to become broad and flat. It finally gives rise to an epithelium so flat that its existence was long overlooked, and has been denied by so competent an observer as Goette; and yet in its flattened condition it possesses to a remarkable degree the capacity of sending out pseudopodia-like processes, a condition indicative much less of a high degree of differentiation or specialization, than of an unspecialized, primitive or embryonic condition.

I have already stated (page 65) that the region from which the regenerating buds of Cheilostomes arise, although one of flattened epithelium, is one in which many more nuclei persist than elsewhere in the adult (cf. again Fig. 71). This fact, coupled with the constancy of position of regenerating buds with reference to the degenerated polypide, is to my mind evidence against the assertion that buds arise here from "*histologically very definitely differentiated tissue.*"

As for regeneration in Endoprocta, no one is more competent to speak than Seeliger himself. I am the more surprised, therefore, to find that in Ascopodaria macropus, which is quite closely allied to the species studied by Seeliger ('89), the cells at the part of the stalk immediately below the "head," from which regenerated buds arise, are, as Ehlers's magnificent Pedicellina work shows, very large and cuboidal (Ehlers, '90, Taf. II. Figs. 26–33). I think one may conclude that a similar condition obtains in some cases in Pedicellina, even judging from Seeliger's own drawings, although they are drawn to a scale that is not quite large enough to allow of settling this point (Seeliger, '89, Taf. X. Fig. 35, *a*, Fig. 41, etc.).

If the increase in size of the flattened cells, and their subsequent rapid division and invagination to form a bud, are due to their more active nourishment, it would be difficult to see why certain cells of any region should quickly undergo this modification, while the adjacent cells apparently as favorably situated with reference to the acquirement of food retain their flattened, quiescent condition, if we assumed such favorable situation to be the only requisite. Still less satisfactorily would such an assumption explain the regular position of regenerating buds. It is taking only one step farther back, but, to my mind, a helpful step, to assert that cell proliferation in any region which produces invagination depends upon the capacity of the cells of that region to become better nourished than their fellows. This may evidently be effected by a diminution in the feeding capacity of the surrounding cells, or by an increase in this respect in the growing cells.

IV. Relationships of Endoprocta and Ectoprocta.

I discussed this topic in my earlier paper (Davenport, '90, pp. 132, 133). I have only to add, that later studies have confirmed my opinion of Nitsche's correctness in placing these two groups close together, and in regarding the Endoprocta as nearer the ancestral types. The stages of Figures 25 (Plate III.) and 77 (Plate IX.) probably represent roughly a phylogenetic stage ancestral to both groups of Bryozoa, but most clearly allied to adult Endoprocta. The formation of new tentacles anteriorly and posteriorly in Figure 77, would reproduce the adult Endoproct condition. Two changes lead to the Ectoproct stage: first, the closure of the tentacular corona posteriorly *in front* of the anus (Plate V. Fig. 43), and, secondly, the formation of the pharynx or anterior part of the œsophagus by the growth of the oral tentacles over the floor of the atrium towards the atrial opening. Thus the brain, which lies at the floor of the atrium in Ectoprocta, comes to lie on the pharynx. The pharynx would, upon this assumption, be a new structure, not found in Endoprocta. Such appearances as are exhibited by Figure 77 lead me to retract my former expressed opinion, in which I agreed with Nitsche in saying that the earliest condition of the tentacular corona is a U-shaped one. Rather, the tentacles are formed first on each side of the atrium, and only secondarily grow around the mouth in front, as later they grow in between mouth and anus. The U-shaped stage is therefore not the primary one, but secondary.

The close relationship of Endoprocta and Ectoprocta has recently been doubted by Cori ('90, p. 16), but his chief argument depends upon the dissimilarity of the Endoproct and Ectoproct kidney. Unfortunately, our knowledge of the latter is still very imperfect, and we may well hope for renewed researches in the subject by this skilful investigator.

Ehlers ('90, pp. 149–154) has recently re-expressed his former ('76, p. 132) utterances concerning the lack of homology between the tentacles of Ectoprocta and the "cirri" of Endoprocta. He finds the homologue of the latter in the "Diaphragma" or "Kragen" of Ectoprocta. This is the organ which I have believed to be homologous with Kraepelin's "Randwulst" (which may be Anglicized as marginal thickening), — an organ occurring in all Ectoprocta. It is nothing but the "neck of the polypide," which has sunk below the general level of the body wall. It is always provided with sphincter muscles, and in Ctenostomes forms the base of insertion of the cylindrical or comb-like "collare setosum." It can hardly be that Ehlers refers to this latter structure by the term "Kragen," since this is merely cuticular. In my opinion the "Diaphragma" of Nitsche cannot be homologized with the cirri of Endoprocta, because it is merely a part of the body wall comparable to that part from which the "polypide" of Endoproctous Bryozoa arises, and *beneath* which the tentacles or "cirri" arise. This part of the body wall is provided with a sphincter in Endoprocta as well as Ectoprocta, and by it the atrial cavity may in both cases be closed.

To my mind, the most significant difference between the two groups exists in the fact that the outpocketing to form the stomach arises from the oral end of the future alimentary tract in Endoprocta, and from the anal end in Ectoprocta. One is led to believe that in the ancestral form either two nearly equally important outpocketings from both the oral and anal sides existed, or that the two existing methods are remnants of a method different from either (such as the formation of the whole alimentary tract at once), or, finally, that the Endoproct condition represents the ancestral one, and that the rectal evagination has secondarily become of greater importance in Ectoprocta, and that the oral evagination has become less significant. Oka ('90, pp. 134, 141) has recently asserted that in the polypide buds of the statoblast and adult colony of a Pectinatella of Japan (P. gelatinosa) the œsophagus and stomach are formed by one evagination, which acquires secondary connection with the rectum. This condition reminds one, then, of Endoprocta. I must, however, doubt the accuracy of Oka's conclusions until more satisfactory evidence is forthcoming; the more so, since Pectinatella magnifica, Leidy, presents a method of budding exactly comparable to that in Cristatella and Plumatella, as my own sections show with sufficient clearness.

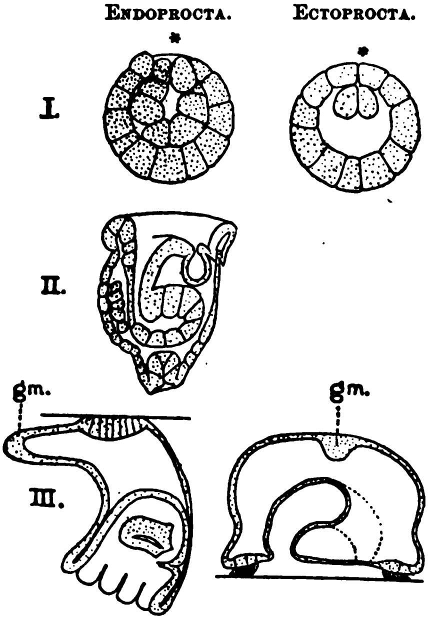
The homology of the Ectoprocta and Endoprocta implies a homology of their larvæ, and demands that the life history of the two groups should be directly comparable.

It is well known from the researches of Hatschek ('77) on Pedicellina, and of Harmer ('85) on Loxosoma, that the surface of the larva which bears the mouth and anus, i. e. its oral side, corresponds with that of the blastopore. How, then, is the oral aspect of the Ectoproct larvæ, which I have tried to show is opposite to the pole of the blastopore, to be homologized with this?

The mouth and anus of the Endoproct larva undergo a rotation after the larva has settled, so that they come to occupy the pole opposite to that at which the blastopore was. This stage of the Endoproct larva is comparable to the whole larval stage of Ectoprocta. I believe the two stages to be homologous, and that, just as polypides are *precociously* formed upon the Phylactolæmatous larva, its larval digestive tract having dropped out from the ontogeny, so the mouth and anus of Gymnolæmata are *precociously* formed on the pole opposite the blastopore, the primitive stage during which they existed at the blastoporic pole having dropped out of the ontogeny.

It is well known from the works of Harmer ('86) and Seeliger ('89), that in Pedicellina, in which the metamorphosis of the larva has been best studied, the stolon arises from the base of the stalk — that is, at the pole where mouth and anus were first formed — at the pole of invagination. I have shown that this is true for Phylactolæmata, and probably for Gymnolæmata.

If the interpretation which I have put on Gymnolæmatous ontogeny becomes confirmed, the larvæ and the budding areas will be homologous throughout all Bryozoa. The following diagrams will explain my idea of the relation of the different ontogenetic stages in the two groups.



The left hand vertical series represents stages in the development of Endoprocta; the right hand one, stages of Ectoprocta. The blastopore (*) is throughout turned upwards in the figures. Stage I. is in both cases a young gastrula. Stage II. is that of the free-swimming larva of Endoprocta. This stage is lost in the ontogeny of Ectoprocta, in which, by abbreviation of larval life, the free-swimming stage corresponds to the condition of the fixed Endoproct after it has undergone its rotation. This stage, or one slightly later, is shown in III. Both larvæ are fixed, the Endoproct by the blastoporic, the Ectoproct by the opposite pole. The position of the stolon, or of the first polypide of the colony produced by non-sexual methods, is represented at *gm.*, near the blastoporic pole.

Summary.

The following general scheme of the budding process in Ectoprocta, derived from my own and other recent studies, may be now drawn up. The references are to pages of this paper.

All Ectoprocta build stocks or corms. The individuals in these are arranged in rows radiating from a centre, — the larva or statoblast, — and are placed one in front of another (Figs. 2, 64ª, 65ª, 67, 71ª, etc.).

New rows or branches are constantly being produced peripherally. There is no dichotomy in the branching (page 86), but the ancestral or median branch gives rise to one or more lateral branches, which in turn become median branches of their part of the stock.

The body wall and polypides of the median branch, as well as the *Anlagen* of lateral branches, arise from a pre-existing mass of embryonic tissue, the gemmiparous mass (pages 72–82). This may exist centrally of the forming region, as in Phylactolæmata, or peripherally, as in Gymnolæmata.

The anal aspect of the polypide is turned towards the gemmiparous mass (page 82).

The outer layer of the body wall in the budding region is one of rapidly assimilating and rapidly dividing tissue; the inner layer of the body wall becomes filled with food taken from the body cavity in species in which the latter is early cut off by a partition (Paludicella, Bowerbankia, Lepralia ?); it shows no tendency to do so in species with a cœnocœl (Phylactolæmata, Alcyonidium).

The first impulse to the formation of the polypide is found in the outer layer of the body wall (excepting when this is highly modified, as in Cristatella), and many cells seem to be involved in its formation from the beginning (pages 8, 56).

This outer layer of the body wall is embryonic tissue, derived from the tip of the stock (margin of the corm) as in Gymnolæmata, or from the neck of pre-existing polypides, as in Phylactolæmata. It is the direct descendant of the gemmiparous tissue of the larva, which in turn has been derived from the region around the blastopore, — in Phylactolæmata certainly, in Gymnolæmata probably (pages 8, 11, 12, 69).

The inner layer of the body wall is also embryonic in the budding region, as indicated by the fact that ova arise near the neck of the polypide, in Phylactolæmata at least (page 68).

The outer mural layer becomes the inner bud layer by invagination, with or without the formation of a cavity. In the former case (many

Gymnolæmata) the mouth of the invagination pocket rapidly closes to give rise to the neck of the polypide (page 56). In the latter case, the cavity of the bud arises only secondarily by a separation of its walls (page 18).

By a rapid growth of the walls of the bud, its distal part, in which the alimentary tract is to arise, is formed. Since this rapid growth occurs earlier at the anal side than at the oral, the rectum is formed first, the stomach last (pages 19, 57).

By an approximation of the lateral walls, alimentary tract and atrio-pharyngeal cavity become separated.

The œsophagus arises as a pocket of the atrio-pharyngeal cavity, and secondarily unites with the stomach (pages 19, 58).

The lophophore arises first as two lateral thickenings of the atrio-pharyngeal wall, then as two lateral folds, whose cavity becomes the ring canal (pages 20, 58),

Tentacles appear on the ridge of the lophophoric fold thus established, and like it are formed first at the sides of the polypide, then anteriorly and posteriorly (pages 22, 59).

The posterior end of the lophophoric ridge is the last to be formed, and, in forming, it cuts off the anal part of the atrium from the intertentacular cavity (pages 23, 62).

The compressed intertentacular cavity becomes circular by change in position of the oral tentacles (pages 24, 62).

The ganglion arises as a depression in the floor of the intertentacular room, and becomes included in the pharynx, which is differentiated by the change in position of the oral tentacles (pages 26, 61).

Muscles and funiculi arise from the cœlomic epithelium of both the body wall and the bud (pages 27–31, 63).

The neck of the polypide may sink to a considerable distance below the general level of the body forming the "Randwulst" of Phylactolæmata or " Diaphragma " of Gymnolæmata (pages 31, 63, 103).

The atrial opening first arises at a late period by separation of the cells of the neck.

The communication plate arises in Paludicella as a circular fold of the layers of the body wall, the mesodermal cells at the centre of which become cuticularized. It is not so completely closed as to prevent communication between the cœlomata of the two individuals it separates.

The mesodermal cells of Paludicella become stored with food material before the formation of the communication plate, and yield it up to the rapidly growing bud.

The regenerated polypides, like the marginal ones, arise in Cheilostomes in a definite position, — on the wall of the operculum from tissue left behind to give rise to the polypide, but not wholly used up in its formation. They arise wholly from the body wall, come to lie next to the "brown body," and cause its disintegration.

The more important theoretical conclusions to which I have arrived are : —

a. There is in every stock or corm of Bryozoa a mass of indifferent cell material, which is derived directly from the indifferent cells of the larva or embryo, and whose function is to form the organs of the different individuals, including the polypides. This mass by constant growth and division affords the embryonic material for lateral branches.

b. The form of the stock and interrelation of individuals is in large part controlled by food supply.

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c. The inner layer of the Phylactolæmatous larva represents mesoderm only : the entoderm has become rudimentary through loss of the alimentary function.

d. The polypides arise in Phylactolæmata at the pole of ingression, which is probably homologous with the aboral pole of Gymnolæmata.

e. The inner layer of the polypide bud is composed of cells derived from the rim of the blastopore, and they are to be regarded as still indifferent, and as first becoming differentiated into ectoderm and entoderm in the formation of the young polypide.

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f. Gemmiparous tissue is a rapidly assimilating tissue possessing large nuclei because actively assimilating, and staining deeply because full of food material.

g. The Endoproct and Ectoproct larvæ are to be compared by assuming that the act of rotation of the axes occurring in the former has been leaped over in the ontogeny, the mouth and anus arising at once on the pole opposite the blastopore.

CAMBRIDGE, MASS., June 1, 1891.

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PLATE I.

ABBREVIATIONS.

cev. pyd.	Neck of polypide.	*gn.*	Ganglion.
cta.	Normal cuticula of adult body wall.	*i.*	Inner layer of bud.
		kmp'drm.	Kamptoderm.
cta.'	Cuticula secreted by tip.	*ms'drm.*	Mesoderm.
ec'drm.	Ectoderm.	*mu. pyr.*	Pyramidal muscles.
ex.	Outer layer of bud.	*œ.*	Œsophagus (pharynx).
ga.	Stomach.	*rt.*	Rectum.
gm.	Bud.	*ta.*	Tentacle.

All figures are of Paludicella Ehrenbergii.

Fig. 1. Stock of Paludicella Ehrenbergii, viewed as an opaque object. × 4.5.

Fig. 2. Diagram representing the interrelations of individuals in stock shown in Figure 1. *A–H* are individuals of the ancestral (median) branch; *a, b, c*, etc., lateral branches given off from the ancestral branch to the right; *a', b'*, branches given off to the left; *α, β*, etc., lateral branches of second order given off in the direction of the distal end of the *ancestral* branch; *α', β'*, etc., given off in the direction of proximal end; a_1', lateral branches of third order — to left.

Fig. 2^a. Diagram of another (smaller) stock. Letters have same significance as in foregoing.

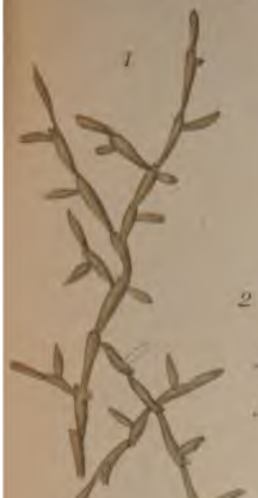
Fig. 3. Cross section of branch near tip, showing the first trace of the bud of the polypide at *ex.*, *i.* × 635.

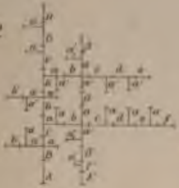
Fig. 4. Cross section of branch near tip, showing bud of polypide slightly older than in Figure 3. × 635.

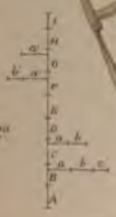
Fig. 5. Cross section of slightly collapsed branch near tip, showing ingression of cells at *ex.* to form inner layer of bud. × 635.

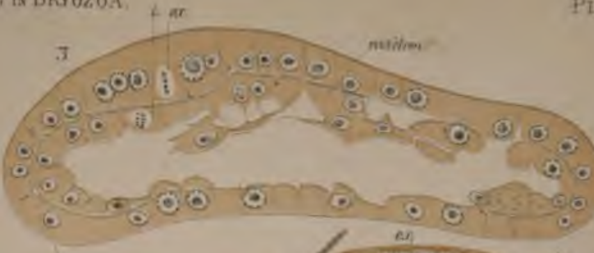
Fig. 6. Longitudinal section of tip of branch to show cell structure. Zeiss, $\frac{1}{18}$ oil immersion, Oc. 1. × 1000.

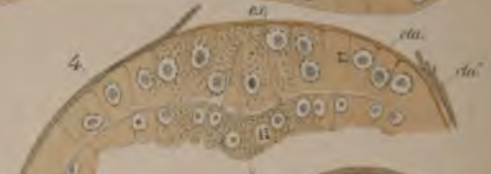
Figs. 7, 8, 9. Optical sections (nearly in sagittal plane) of three tips of branches in successive stages of development, showing relations of young bud, *gm.*, to next older polypide. In Figure 8 the branch is slightly shrunken. × 87.

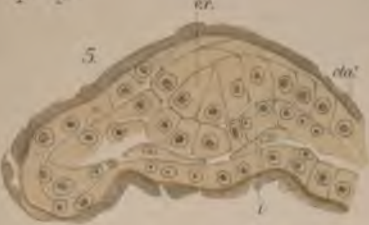


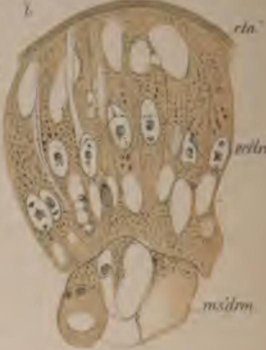


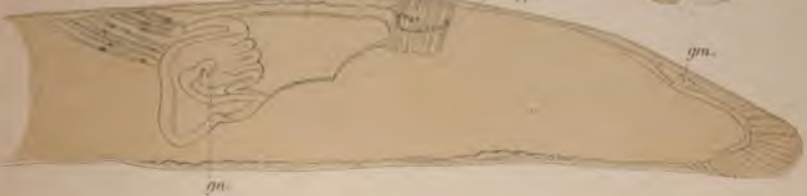


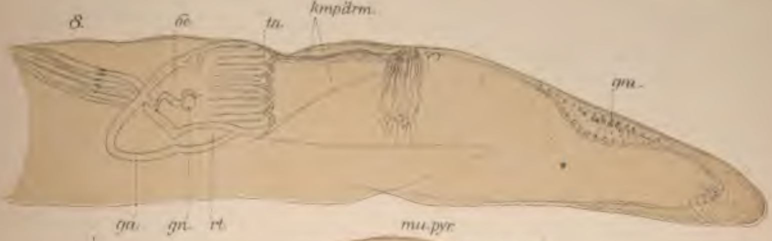


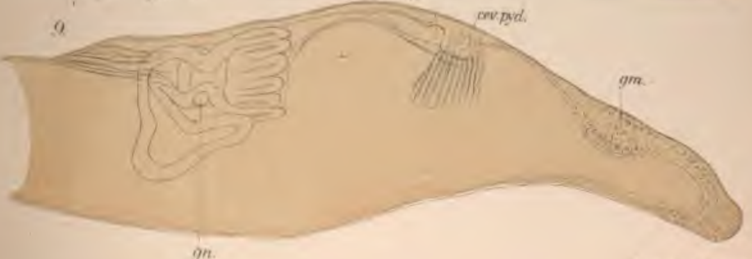












C.B.D. del.

B. Meisel, lith. Boston.

PLATE II.

ABBREVIATIONS.

cev. pyd.	Neck of polypide.	*ec'drm.*	Ectoderm.
cta.	Normal cuticula of body wall.	*gm. l.*	*Anlage* of lateral bud.
		kmp'drm.	Kamptoderm.
cta.'	Cuticula secreted by tip.	*ms'drm.*	Mesoderm.

All Figures from preparations of Paludicella Ehrenbergii.

Fig. 10. Surface view of cuticula near the end of a branch at intervals, *a* being nearest the tip, and *d* farthest from it. The branch was stained in Erlich's hæmatoxylin, the color being taken up by superficial cuticula only. × 320.

Figs. 11, 12, 13. Cross sections of the cuticula taken at different distances from the tip, to show the stainable and non-stainable cuticulæ. Figure 11 is from near the tip, Figure 13 farthest from it. × 1000.

Fig. 14. Longitudinal median (sagittal) section through the tip of a branch showing cells of tip and an early stage in the development of the polypide. × 410.

Fig. 15. Cross section of branch showing origin of lateral bud. × 635.

Fig. 16. Longitudinal section of body wall of branch through the point at which a lateral bud is originating. Polypide of ancestral branch is nearly adult. × 635.

Fig. 17. Longitudinal section of body wall from near the tip through the *Anlage* of a lateral bud. × 410.

Fig. 18. Cross section of branch showing histological conditions of *Anlage* of lateral bud. The polypide has reached a stage of development corresponding to that of Figure 36, Plate IV. × 1000.

Fig. 19. Longitudinal section through body wall from the same branch as Figure 17, but farther from the tip. Histological conditions are to be compared with those of Figure 17, which represents a less differentiated condition. × 410.

Fig. 20. Cross section of branch in which the polypide has reached a stage slightly younger than that of Figure 36. To show *Anlage* of two lateral buds with their cuboidal undifferentiated cells. × 410.

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PLATE III.

ABBREVIATIONS.

An.	Anal side of polypide.	*kmp'drm.*	Kamptoderm.
atr.	Atrium.	*loph.*	Lophophore.
cev. pyd.	Neck of polypide.	*ms'drm.*	Mesoderm.
cl. mu. ret.	Young cells of retractor muscle.	*mu. par.*	Parietal muscle.
		œ.	Œsophagus.
cta.	Cuticula.	*Or.*	Oral side of polypide.
ec'drm.	Ectoderm.	*rt.*	Rectum.
ga.	Stomach.	*vlv. cr.*	Cardiac valve.
gn.	Ganglion.		

All figures from preparations of Paludicella Ehrenbergii.

Figs. 21–25. Longitudinal sections through buds of polypides at successively older stages. The tip of the colony, and therefore the anal aspect of the polypide, is to the right in all cases. All figures × 410.

Fig. 21. Stage of Figure 37 (Plate IV.). Few nuclei in central region.

Fig. 22. Shows rapid growth of bud, chiefly at neck of polypide. The two inner cell layers are about to separate to form the common cavity of atrium and œsophagus.

Fig. 23. Beginning of formation of alimentary tract at rectum, *rt.* The row of nuclei separating the atrio-œsophageal cavity from the alimentary tract is due to the fusion of the two inner layers of the bud along this line.

Fig. 24. Rectum and stomach completed. Retractor muscles begin to form.

Fig. 25. Lophophore and young tentacles have made their appearance, and œsophagus and pharynx are separated from atrium. Beginning of formation of brain at *gn.*

Fig. 26. Part of cross section of a branch of stage of Figure 30. Parietal muscles, *mu. par.*, occupy a diameter of the section, and are attached to the cuticula. × 635.

Fig. 27. Young parietal muscle at stage of Figure 28. This is one of the pair which in a later stage are found lying together in Figure 26. × 635.

Fig. 28. Cross section of branch showing young polypide, and reticulated vacuolated cells. × 410.

Fig. 29. Bit of body wall, with cuticula separated from underlying ectoderm to show ends of parietal muscles. × 690.

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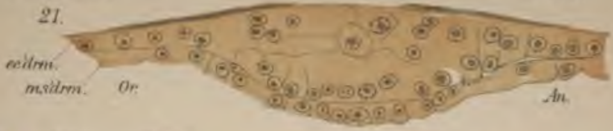

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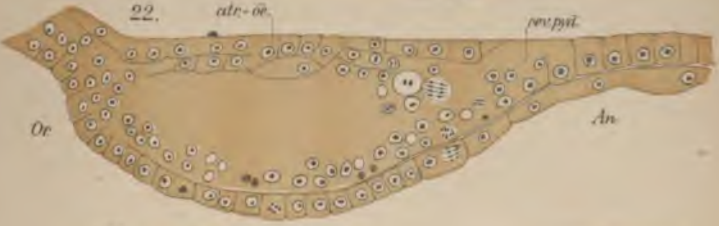

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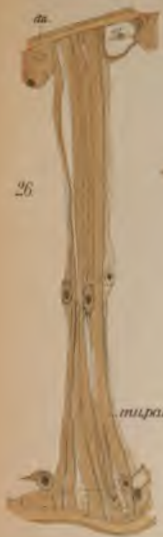

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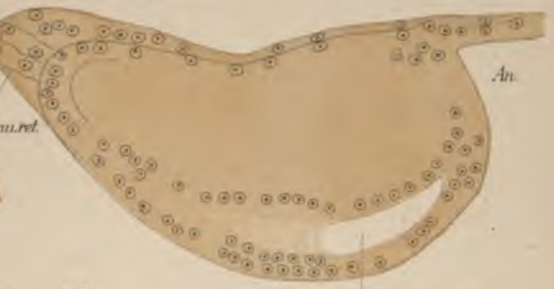

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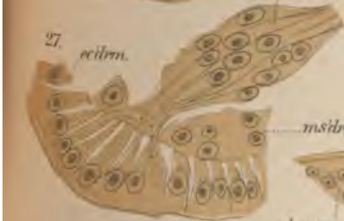

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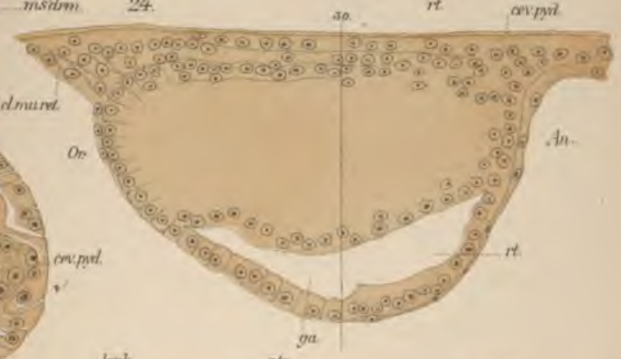

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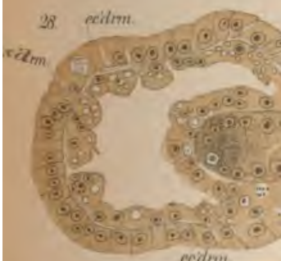

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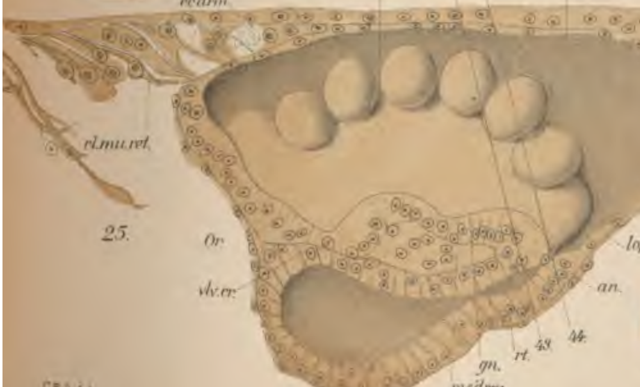

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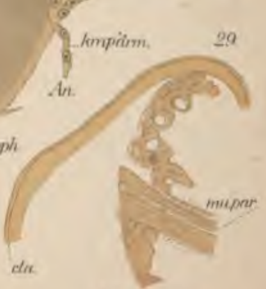


C.B.D. del.

B. Meisel, lith. Boston.

PLATE IV.

ABBREVIATIONS.

An.	Anal side of polypide.	*i.*	Inner layer of bud.
an.	Anus.	*loph.*	Lophophore.
atr.	Atrium.	*ms'drm.*	Mesoderm.
can. crc.	Ring canal.	*mu.*	Muscle fibre in funiculus.
ec'drm.	Ectoderm.	*n.'*	Circumœsophageal nerve.
ex.	Outer layer of bud.	*œ.*	Œsophagus.
fun. inf.	Inferior funiculus.	*Or.*	Oral side of polypide.
fun. sup.	Superior funiculus.	*rt.*	Rectum.
ga.	Stomach.	*vac.*	Vacuole.
gn.	Ganglion.	*vlv. cr.*	Cardiac valve.

All figures from preparations of Paludicella Ehrenbergii.

Fig. 30. Cross section of polypide bud of stage of Figure 24, Plate III. The position is indicated by the line 30, Figure 24. × 410.

Figs. 31–34. Four cross sections of a branch through a young polypide, somewhat younger than that of Figure 25. Figure 31 is nearer the anal, Figure 34 nearer the oral surface. In Figure 34 that part only of the section of the polypide which lies near the body wall is represented. × 410.

Fig. 35. Cross section of branch through polypide of age of Figure 25. To show origin of tentacles and ring canal. × 410.

Fig. 36. Sagittal section of young polypide at period of closure of ganglion, *gn.* × 410.

Fig. 36^{a}. Bit of same polypide a few sections to one side of plane of Figure 36, showing origin of inferior funiculus. × 410.

Fig. 37. From cross section of branch showing early stage in development of the bud. × 410.

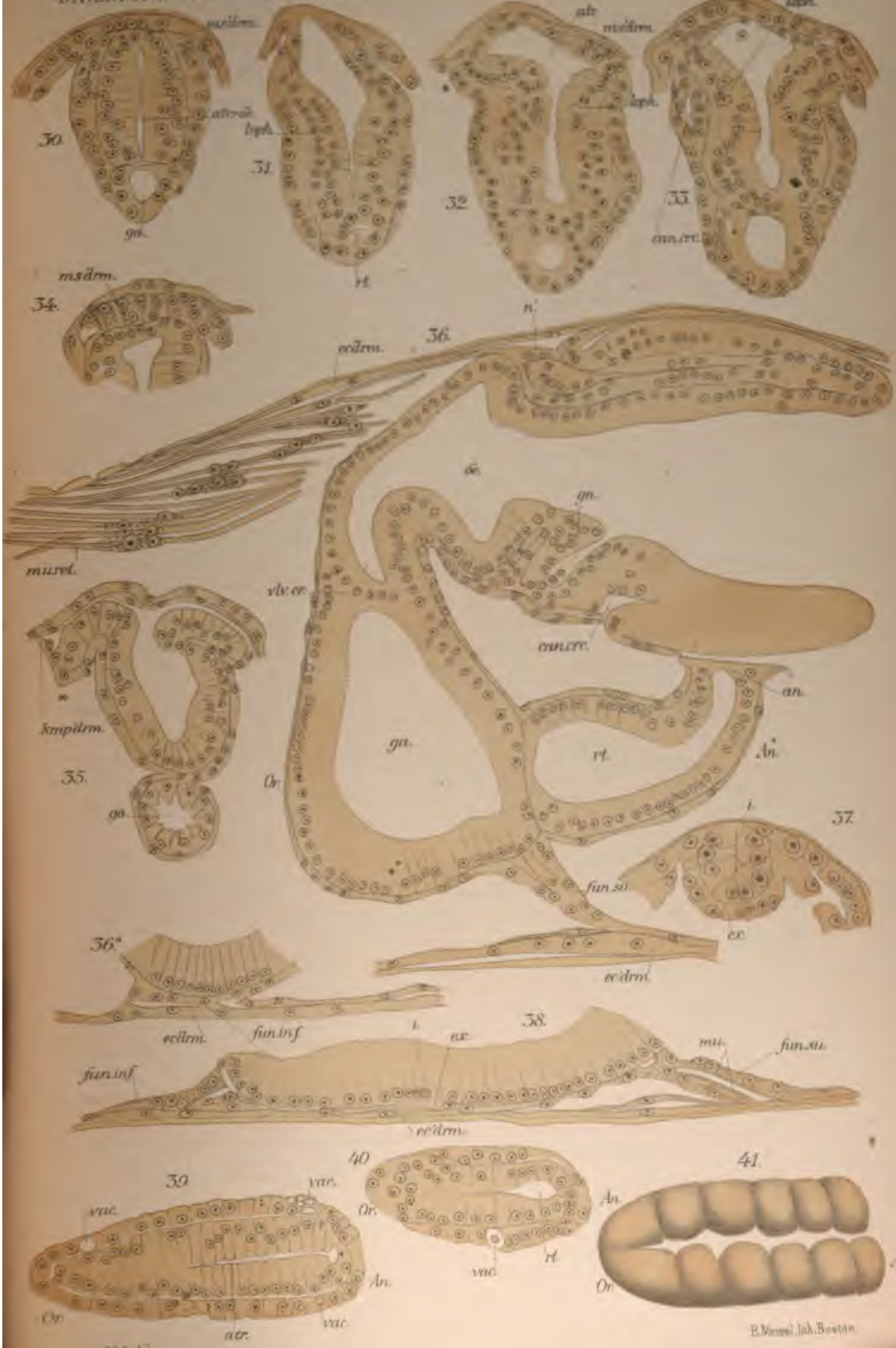
Fig. 38. From a sagittal section of nearly adult polypide, showing the two funiculi and their muscles. × 410.

Figs. 39 and 40. Two neighboring sections parallel to the body wall through a bud of the stage of Figure 23. Figure 40 lies three sections below Figure 39. Figure 39 shows the atrial cavity, formed as yet only on the anal side. Figure 40 shows the beginning of formation of the alimentary tract at the anal end. Note the vacuolated condition of the mesoderm. × 410.

Fig. 41. Polypide of about the stage of Figure 25 looked at *en face.* The anal tentacles, being turned under, do not appear. To show compressed condition of polypide, and alternating position of tentacles. Cf. Figure 77, Plate IX. × 320.

DAVENPORT – BUDDING IN BRYOZOA.

PL. IV.



C.B.D. del.

B. Meisel, lith. Boston.

PLATE V.

ABBREVIATIONS.

an.	Anus.	*kmp'drm.*	Kamptoderm.
cev. pyd.	Neck of the polypide.	*loph.*	Lophophore.
clr. set.	Collare setosum.	*ms'drm.*	Mesoderm.
cta.	Normal cuticula of adult body wall.	*mu. par.*	Parietal muscles.
		mu. pyr.	Pyramidal muscles.
cta.'	Cuticula secreted by the tip of branch.	*of. atr.*	Atrial opening.
		rt.	Rectum.
ec'drm.	Ectoderm.	*spht.*	Sphincter.

All figures from preparations of Paludicella Ehrenbergii.

Fig. 42. Cross section of branch of age of Figure 37, Plate IV., to show origin of primary parietal muscles. × 410.

Figs. 43 and 44. Successive sections through a polypide slightly older than that of Figure 25, cut perpendicularly to the long axis of the branch. During this period the lophophore becomes more nearly circular, and its aboral ends meet oralwards of the rectum, *rt.* Figure 44 is nearer the tip of the branch. × 410.

Fig. 45. Axial section of neck and atrial opening of polypide just sufficiently developed to be capable of extrusion. Shows the collare setosum in place. × 410.

Fig. 46. Section of communication plate cut across the branch. Two sections (10 μ) above Figure 51. × 635.

Figs. 47–49. Three stages in the development of the communication plates. Longitudinal sections of the branch. In Figure 47, the polypide has reached the stage of Figure 22; in Figure 48, the stage of Figure 23; and in Figure 49, the stage of Figure 24. × 635.

Fig. 50. Longitudinal section through neck of young polypide, showing the sinking of the neck below the general surface of the body, and the method of forming the inner cuticula of neck. × 390.

Fig. 51. Cross section of branch through communication plate. The left side of the section includes the cuticula and the underlying flat ectodermal layer. The right side cuts a little lower into the mesodermal cells. × 635.

PLATE VI.

ABBREVIATIONS.

an.	Anus.	*i.*	Inner layer of bud.
can. crc.	Ring canal.	*kmp'drm.*	Kamptoderm.
cev. pyd.	Neck of the polypide.	*la. comn.*	Communication plate.
cl. rtl.	Reticulated cells.	*ms'drm.*	Mesoderm.
cta.	Normal cuticula of adult body wall.	*mu. par.*	Parietal muscles.
		mu. pyr.	Pyramidal muscles.
cta.'	Cuticula secreted by tip.	*n.'*	Circumœsophageal nerve.
ec'drm.	Ectoderm.	*œ.*	Œsophagus.
ex.	Outer layer of bud.	*rt.*	Rectum.
gm.	Bud.	*vac.*	Vacuole.
gn.	ganglion.		

All figures from preparations of Paludicella Ehrenbergii.

Fig. 52. Cross section of a branch through a polypide slightly older than that shown in Figure 36. The section passes through the brain and whole extent of the ring canal, together with its opening into the cœlom. × 635.

Fig. 53. Next section below Figure 52 of same series; showing the beginning of the circumœsophageal nerve ring. × 635.

Fig. 54. Shows connection of mesodermal cells of body wall, *ms'drm*, with those of the outer layer of bud, *ex*. × 1030.

Fig. 55. Origin of the secondary parietal muscle cells from mesoderm of body wall. × 635.

Fig. 56. Histological conditions of the budding regions. The cells have large nuclei, the mesodermal cells are vacuolated and rapidly dividing; the cells of the bud are densely granular. Zeiss, $\frac{1}{18}$ oil immersion, Oc. 1. × 1070.

Fig. 57. Normal vacuolated cell, full of food particles. × 1030.

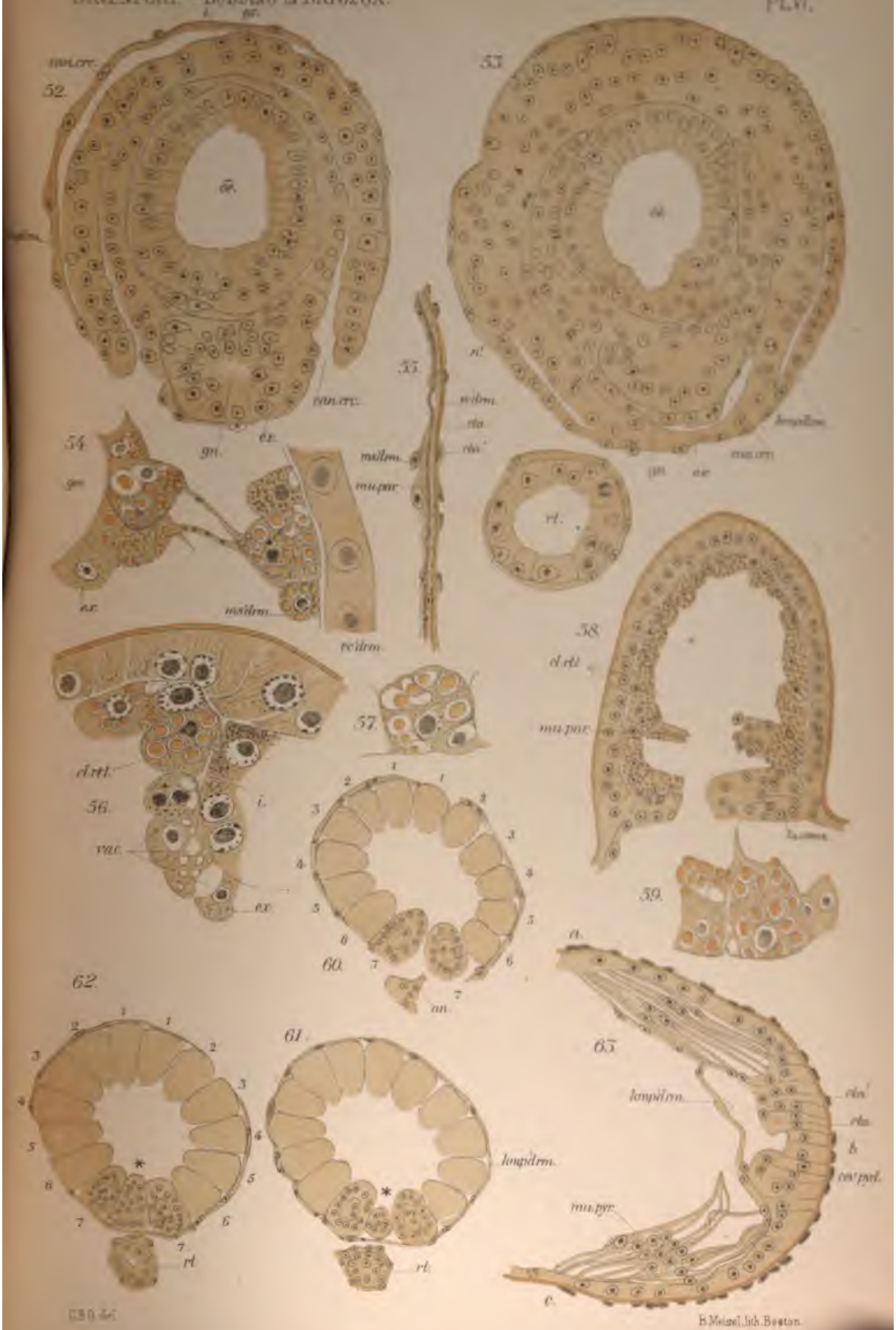
Fig. 58. Longitudinal section of young lateral branch, showing highly reticulated character of mesoderm, and nearly complete formation of communication plate. × 410.

Fig. 59. Reticulated cell, showing one of the pseudopodia-like processes which frequently appear on them, projecting into the cœlom. × 1030.

Figs. 60–62. Three successive sections from a series across the tentacles of a polypide which has 15 tentacles, and is of about the stage of Figure 36. The odd tentacle (*) is shorter than the others, and lies opposite the rectum, *rt*. × 295.

Fig. 63. Cross section of branch through neck of polypide of about the age of Figure 36. Shows also the young pyramidal muscles. × 410.

DAVENPORT. – BUDDING IN BRYOZOA. PL. VI.



C.B.D. del.

B. Meisel, lith. Boston.

PLATE VII.

For explanation of notation employed on this plate, see page 41.

Fig. 64. Outline drawing of one of the lateral "fans" of *Bugula turrita*, taken from the axis of the colony and spread out flat on the slide. × ca. 12.
Fig. 64ᵃ. Diagram showing arrangement of individuals in Figure 64.
Fig. 65. Outline drawing of one of the lateral branches of a stock of *Crisia eburnea*, spread out flat on the slide. × 16.
Fig. 65ᵃ. Diagram showing arrangement of individuals in Figure 65.
Fig. 66. Part of stock of *Bugula flabellata*. × 10.

Hincks, T.

'80. A History of the British Marine Polyzoa. 2 vols., 8°. (11) + cxli + 601 pp., 83 pls. London, John van Voorst.

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PLATE VIII.

ABBREVIATIONS.

op.	Operculum.	*pyd. rgn.*	Regenerated polypide.
pyd. dgn.	Degenerated polypide.		

Fig. 67. Diagram to show interrelation of individuals in the corm, Figure 69.

Fig. 68. A part of a corm of *Membranipora pilosa*, to show regular arrangement, with a single median branch, each of whose individuals gives rise to two lateral branches. The * indicates margin of frond on which stock was growing. × ca. 8.

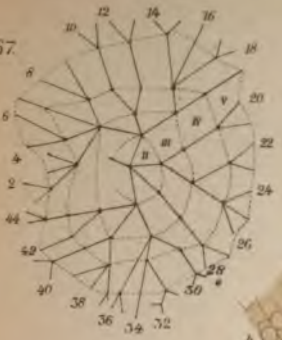
Fig. 69. Young corm of *Flustrella hispida*, to show arrangement of individuals. × 10.

Fig. 70. Young corm of *Membranipora pilosa*, with several median branches, showing regular arrangement. The marginal ones alone give rise to lateral branches. × 10.

Fig. 71. Young corm of *Lepralia Pallasiana*, showing arrangement of individuals. On the left, the nuclei of the cells of the body wall are shown, to indicate the inequality of their distribution. On the right, nuclei are omitted. At *pyd. rgn.* a regenerating polypide is seen, on the operculum. × 43.

Fig. 71^{a}. Plan of Figure 71.

67.



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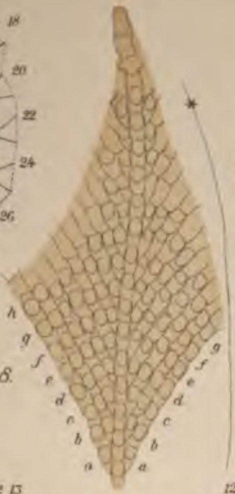

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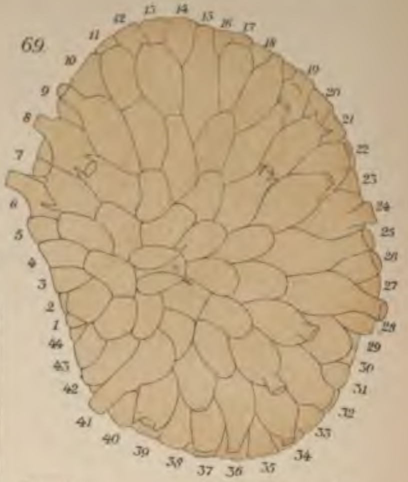

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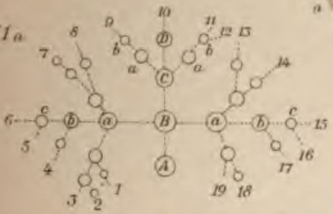

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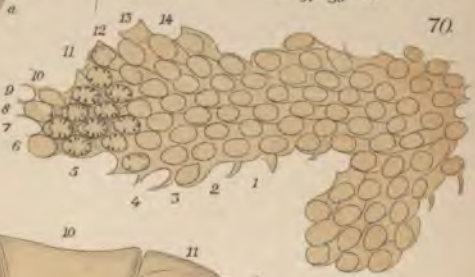

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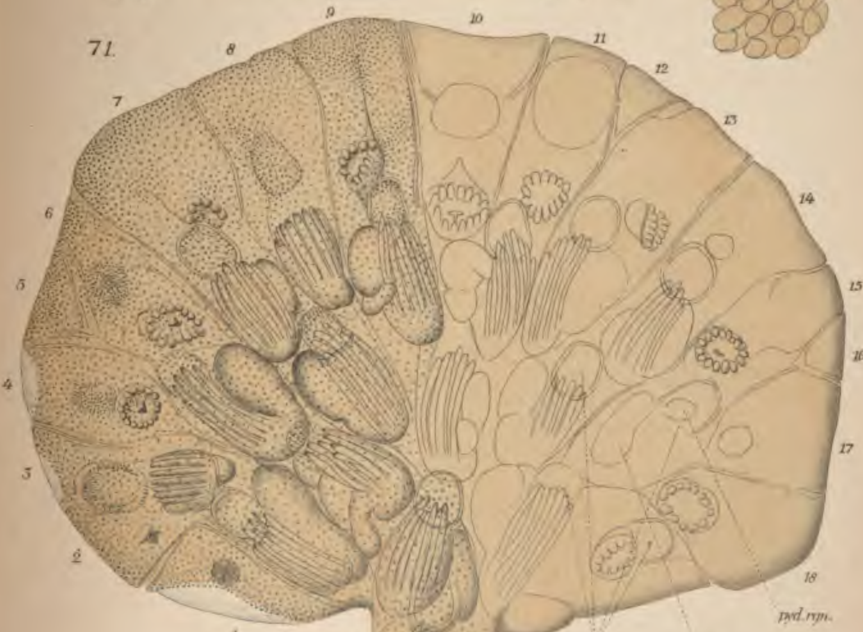


C.B.D. del.

B.Meisel, lith. Boston

PLATE IX.

ABBREVIATIONS.

An.	Anal side of polypide.	*lu. gm.*	Lumen of bud.
atr.	Atrium.	*marg.*	Margin of corm.
can. crc.	Ring canal.	*ms'drm.*	Mesoderm.
cev. pyd.	Neck of the polypide.	*n.'*	Circumœsophageal nerve.
cta.	Cuticula.	*œ.*	Œsophagus.
ec'drm.	Ectoderm.	*Or.*	Oral side of polypide.
ex.	Outer layer of bud.	*rt.*	Rectum.
ga.	Stomach.	*sep.*	Wall of zoœcium in the corm.
gm.	Bud.	*sol.*	Sole of the corm.
gn.	Ganglion.	*tct.*	Roof of the corm.
i.	Inner layer of bud.		

Fig. 72. Longitudinal vertical section through the peripheral part of the corm of *Lepralia Pallasiana,* showing the margin of the corm and two zoœcia, the older of which contains a polypide. × 160.

Fig. 73. Longitudinal vertical section through the margin of a corm of *Lepralia Pallasiana,* showing the two layers of this region and the origin of the polypide. × 410.

Fig. 74. Young regenerating polypide of *Flustrella hispida.* The section passes through the sagittal plane. × 380.

Fig. 75. Vertical section through margin of corm of *Flustrella hispida,* to show origin of polypide. × 410.

Fig. 76. Sagittal section through young polypide of *Flustrella hispida,* to show early stage of development of alimentary tract. × 410.

Fig. 77. Superficial view of young polypide from upper surface of corm of *Flustrella hispida,* showing young tentacles and their relation to the anus (at *atr.*). × 320.

Fig. 78. Bud of polypide of *Flustrella hispida* at the time of closure of the pore of invagination. × 390.

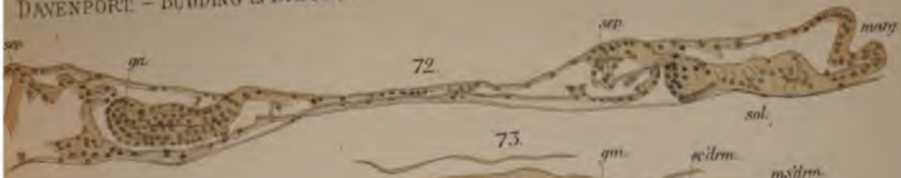
Fig. 79. Radial section through margin of corm of *Flustrella hispida,* showing bud of polypide. × 410.

Fig. 80. Young polypide of *Flustrella hispida.* × 380.

Fig. 81. Bud of *Lepralia Pallasiana* immediately before the formation of alimentary tract, showing relation of the rectal pocket (*rt.*) to the atrio-pharyngeal cavity above. × 410.

Fig. 82. Section through polypide, through lately formed brain and circumœsophageal nerves (*n.'*) growing around œsophagus (*œ.*). × 410.

72.



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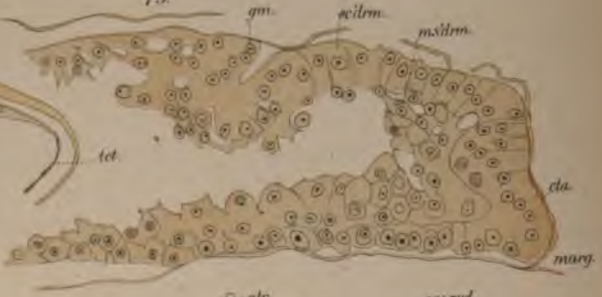

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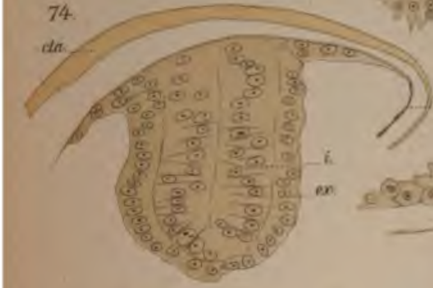

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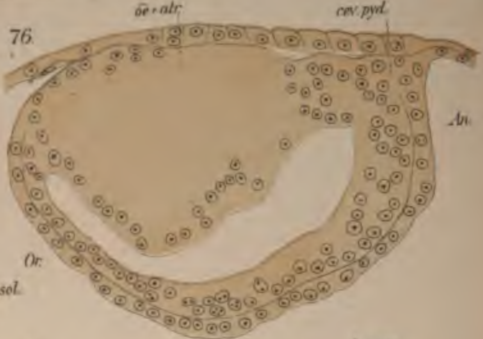

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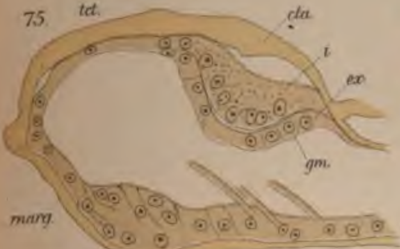

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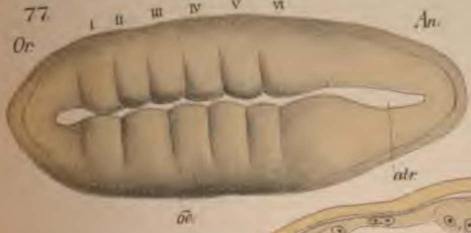

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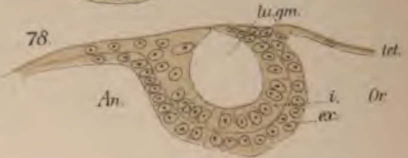

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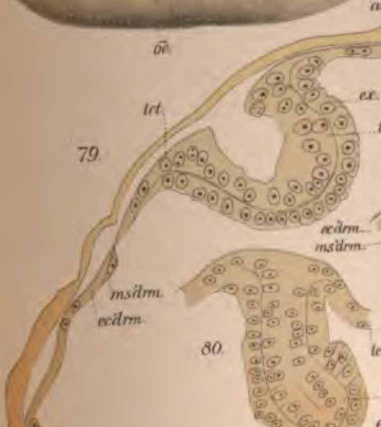

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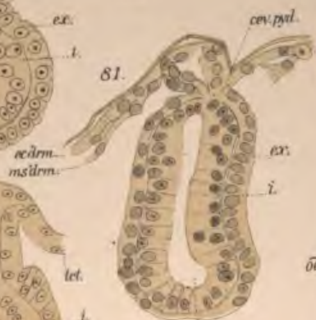

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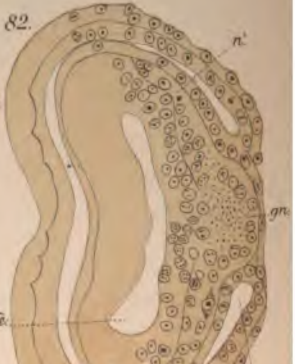


C.B.D. del.

B Meisel, lith. Boston.

PLATE X.

ABBREVIATIONS.

An.	Anal side of polypide.
an.	Anus.
atr.	Atrium.
can. crc.	Ring canal.
cev. pyd.	Neck of polypide.
cœ.	Cœcum.
cta.	Cuticula.
di'sep.	Wall of zoœcium in the corm.
ec'drm.	Ectoderm.
ex.	Outer layer of bud.
fun.	Funiculus.
ga.	Stomach.
gn.	Ganglion.
i.	Inner layer of bud.
kmp'drm.	Kamptoderm.
lu. gn.	Lumen of the ganglion.
ms'drm.	Mesoderm.
mu.	Musculature of œsophagus.
mu. ret.	Retractor muscle of polypide.
œ.	Œsophagus.
op.	Operculum.
Or.	Oral side of polypide.
or.	Mouth.
pyd. dgn.	Degenerated polypide, "brown body."
rt.	Rectum.
ta.	Tentacle.

Fig. 83. Sagittal section through young polypide of *Escharella variabilis.* × 320.

Fig. 84. Regenerated polypide of *Lepralia Pallasiana* on operculum (*op.*). × 380.

Fig. 85. Cross section of pharynx of adult polypide of *Escharella variabilis*, showing perforated cell walls. × 635.

Fig. 86. Sagittal section of young polypide of *Lepralia Pallasiana*, showing formation of brain. × 320.

Fig. 87. Section parallel to sole of a corm of *Escharella variabilis* at about the stage of Figure 86, showing atrium, ganglion, and rectum. × 430.

Fig. 88. Vertical section through a bit of roof of corm of *Escharella variabilis* at neck of polypide, showing also the region of future operculum and of origin of future regenerated buds. Compare with Figure 90. × 410.

Fig. 89. Sagittal section of young regenerated polypide of *Flustrella hispida* intermediate in age between Figures 86 and 83. Shows the origin of the ganglion and rotation of the oral tentacles. × 320.

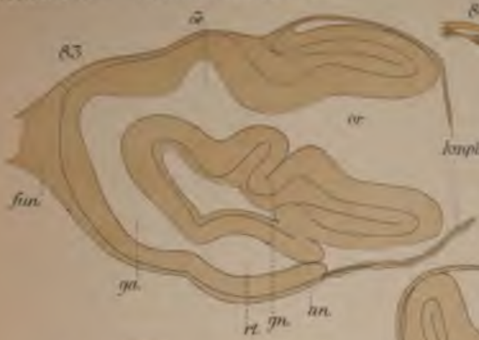
Fig. 90. Vertical section of a bit of body wall from same individual as Figure 88, to show the comparatively less embryonic condition of cells here than at neck of polypide. × 410.

Fig. 91. Operculum of *Lepralia Pallasiana* cut perpendicularly to surface, showing origin of a regenerating polypide. Body wall somewhat shrunken from cuticula. × 410.

Fig. 92. Section through a regenerated polypide of *Escharella variabilis*, showing relations of alimentary tract to "brown body" (*pyd. dgn.*). × 410.

DAVENPORT — BUDDING IN BRYOZOA. PL. X.

83.



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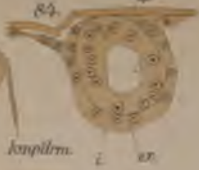

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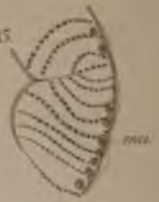

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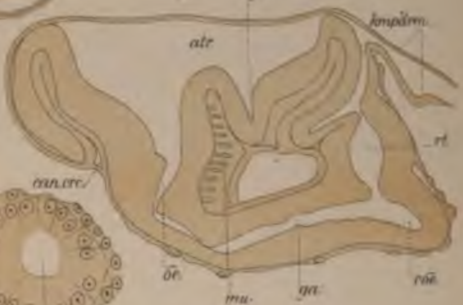

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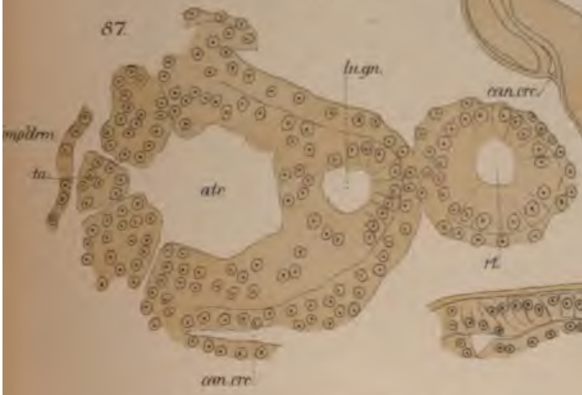

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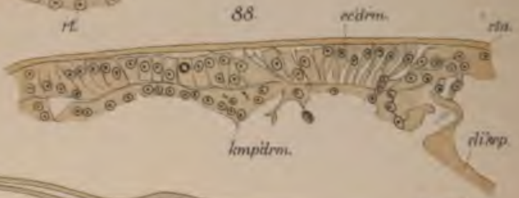

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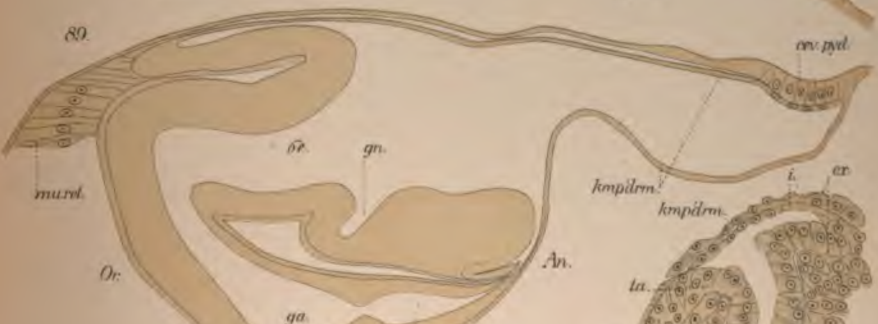

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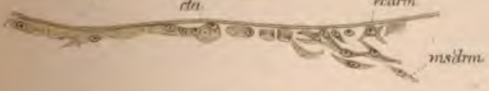

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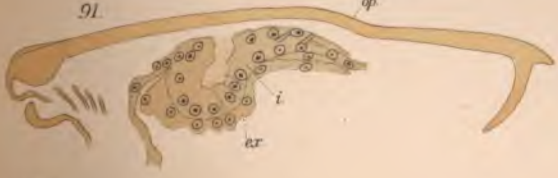

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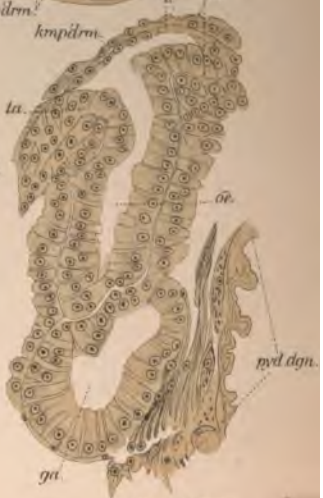


C.B.D. del.

B. Meisel, lith. Boston.

PLATE XI.

ABBREVIATIONS.

cev. oœ.	Neck of oœcium.	*ms'drm.*	Mesoderm.
cœl.	Cœlom.	*oœ.*	Oœcium.
ec'drm.	Ectoderm.	*ov.'*	Oöblasts.
en'drm.	Entoderm.	*pyd.*	Polypide.
ex.	Outer layer of bud.	*sto.*	Stolon.
i.	Inner layer of bud.	*tct.*	Roof of stock.
lu. gm.	Lumen of the bud.		

Fig. 93. A portion of a longitudinal section through a young stock of *Plumatella polymorpha*, about two weeks after hatching from statoblast (killed 12th May, 1890), showing the body wall just analward of the neck of a young polypide (*pyd.*), at the oral side of which a younger bud has already arisen. The inner (mesodermal) layer of the body wall shows oöblasts (*ov.'*) in various stages of development. × 600.

Fig. 94. Longitudinal section of oœcium of *Cristatella* showing embryo which is giving rise to the cœlomic epithelium by ingression of cells at its proximal pole, — i. e. the pole nearest the neck of the oœcium. There are in the next section two other cells in the cavity of the blastula, one of which appears degenerate in that it contains a huge vacuole, and has no distinct nucleus, the chromatic substance lying scattered loose near the cell wall. × 600.

Fig. 95. Longitudinal section through oœcium of *Cristatella* and its contained embryo. One polypide bud and the stolon (*sto.*) are shown here. There are two other buds in the embryo further developed than this one, lying to one side of it, and on the side of each of these buds is the *Anlage* of another. The *stolon* is seen to be well developed, lying between the ectoderm and mesoderm throughout the region bounded by the three older buds, and extending as a zone beyond them, and even beyond the *Anlage* of the youngest polypides. The embryonic tissue thus forms a disk about 75 × 150 μ in extent. × 390.

Fig. 96. Transverse section of oœcium of *Plumatella*, showing origin of first polypide. Compare with Figure 99, which represents an earlier stage. × 390.

Fig. 97. Longitudinal section through oœcium and contained embryo of *Cristatella*. The stolon is already cut off from the ectoderm. This stage immediately follows that of Figure 101, Plate XII. The forming bud is that of the first polypide. × 390.

Fig. 98. Oblique section through oœcium of *Plumatella*, showing a later stage in development of the inner layer of the larva (cf. Fig. 94). × 600.

Fig. 99. Longitudinal section of oœcium and contained larva of *Plumatella*. The bud shown at *i.*, *ex.* is the first in the colony. An incipient (second) bud is shown five sections to one side in the region indicated by an asterisk. × 410.

PLATE XII.

ABBREVIATIONS.

ec'drm.	Ectoderm.	*ms'drm.*	Mesoderm.
ex.	Outer layer of bud.	*oœ.*	Oœcium.
i.	Inner layer of bud.	*sto.*	Stolon.
lu. gm.	Lumen of the bud.		

Fig. 100. Longitudinal section of a larva of *Plumatella polymorpha,* in which the two layers are established; the pole of ingression is directed upward, on the plate.

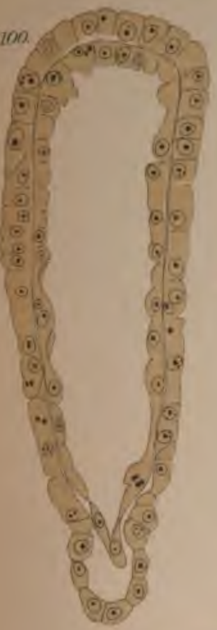
Fig. 101. Section of upper part of zoœcium of *Cristatella mucedo,* with its contained larva. Showing the formation of the stolon at the pole of ingression and the attachment of this pole to the placenta-like neck of the oœcium (*). × 390.

Fig. 102. Section through an oœcium of *Cristatella,* with its contained larva. One polypide is already established, and a second is arising. The two are the only buds in the larva. On the left of the older bud the stolon is seen to be intruding itself between the ectoderm and mesoderm of the larva. × 390.

Fig. 103. Section through the two oldest polypides of the *Cristatella* larva, together with the stolon. This larva contains one other less developed bud at one side of these two. × 390.

Fig. 104. *Plumatella polymorpha.* Stage of first bud later than that shown in Figure 96, exhibiting pore of invagination closed by overgrowth of ectoderm. × 390.

100.



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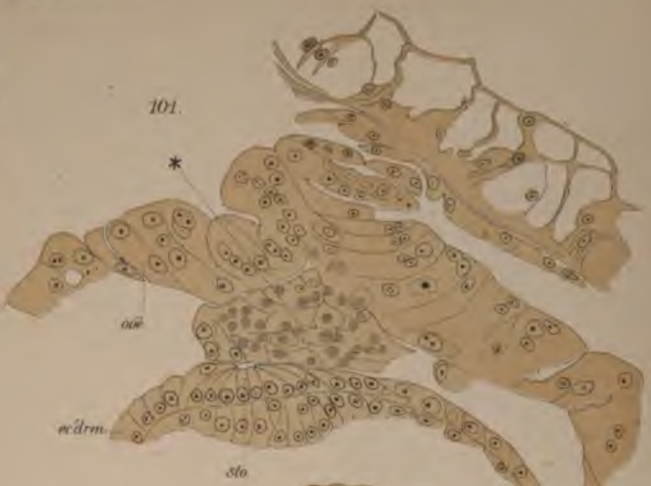

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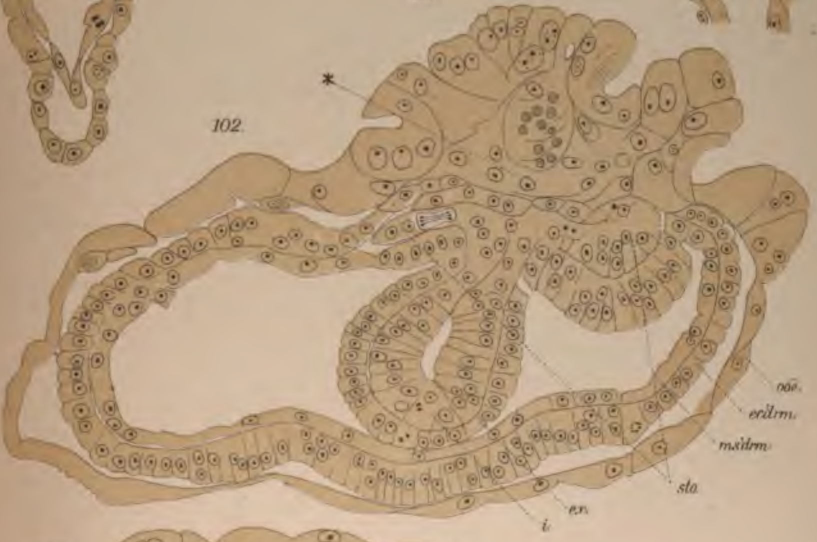

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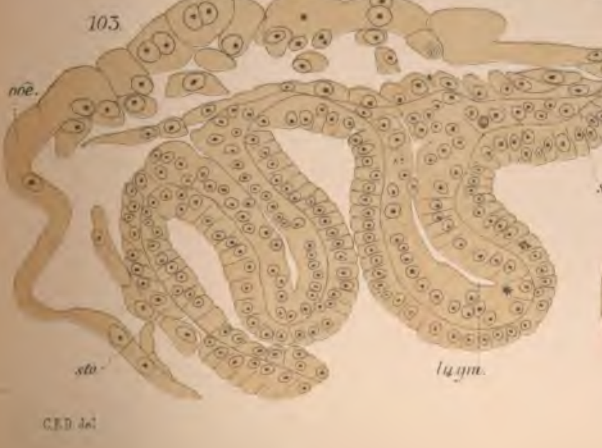

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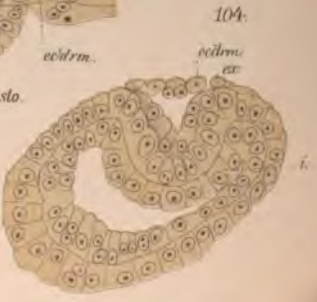

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